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Behavioral and Physiological Adaptations of Largemouth Bass (Micropterus Salmoides) to Low-Salinity Environments.

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Behavioral and physiological adaptations of largemouth bass (*Micropterus salmoides*) to low-salinity environments

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BEHAVIORAL AND PHYSIOLOGICAL ADAPTATIONS OF LARGEMOUTH BASS (*Micropterus salmoides*) TO LOW-SALINITY ENVIRONMENTS

A Dissertation

Submitted to the graduate faculty of the
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by
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ABSTRACT

A study of the biology, movements, behavior, and physiology of largemouth bass (Micropterus salmoides) from a low-salinity marsh in Lafourche Parish, Louisiana was conducted from March 1985 to December 1987. Comparative data were also collected for freshwater largemouth bass from Ben Hur Lake and False River, Louisiana.

Marsh largemouth bass were small compared to freshwater bass of similar age, although growth rates of older marsh bass equaled or exceeded those of freshwater fish. Marsh bass relative weight indicated excellent condition during all seasons, while freshwater bass exhibited reduced condition in early spring and fall. Characteristic body morphology and growth of marsh bass suggest an adaptation to low-salinity environments.

Salinity did not influence daily movements of ultrasonically-tagged largemouth bass, although salinity increases in late summer may have induced large-scale seasonal movements. Though tagged fish could not be located after salinities reached 8 parts per thousand (ppt), largemouth bass smaller than tagged individuals were collected in the study area. The presence of large predators combined with potential stressful physicochemical conditions may influence movements of largemouth bass in low-salinity environments.

Salinity preferences of adult and young-of-the-year (YOY) largemouth bass indicated YOY marsh and freshwater bass preferred 0 ppt. Although adult marsh and freshwater bass preferred 3 ppt, mean number of observations at 0 ppt was significantly greater for freshwater bass, while mean number of observations at 3 ppt was significantly greater for

marsh bass. Differences in salinity selection by adult largemouth bass between collection sites may be the result of long-term exposure to salinity.

Experiments in which marsh and freshwater largemouth bass were exposed to 0, 4, 8, and 12 ppt salinity indicated no significant differences in plasma osmolalities, electrolyte concentrations, or gill ATPase activities between marsh and freshwater fish exposed to 0, 4, or 12 ppt. Exposure to 12 ppt resulted in osmotic stress in largemouth bass from both collection sites. At 8 ppt, marsh bass had significantly higher plasma chemistry values and lower gill ATPase activities than freshwater fish. Marsh bass appear to have adapted to environments of variable salinity by reducing energetic expenditures related to osmoregulation.

CHAPTER 1. INTRODUCTION

The largemouth black bass, Micropterus salmoides (Lacepede) is one of the most abundant and sought after gamefish in North America (U.S. Department of Interior 1982). This species has been extensively stocked in lakes, reservoirs, and ponds in the southeastern United States (MacCrimmon and Robbins 1975) and is the principal gamefish sought by Louisiana fishermen (La. Dept. Wildlife and Fisheries 1980). Although most often found in freshwater habitats, largemouth bass have been collected in brackish water (Hildebrand and Schroeder 1928, Kilby 1955, Keup and Bayless 1964). Such largemouth bass are known by a variety of names including tidal bass, coastal bass, and marsh bass, and contribute to sportfish harvests in coastal areas (Guier et al. 1978, Tucker 1985). Marsh bass can be found from Delaware (R.W. Miller, Supervisor of Finfisheries, Delaware Department of Natural Resources and Environmental Control, pers. comm.) to Louisiana.

Though some survey data are available concerning marsh bass, most reports contain only collection sites and few studies have been conducted since the mid-1960's. Age, growth rates, and condition of largemouth bass in Louisiana have been documented (Brashier 1965, Shay and Ward 1969, Colle et al. 1976), but these studies dealt with inland waters and freshwater marshes. No study has examined movements of largemouth bass in relation to salinity gradients, and physiological adaptations to low-salinity habitats and their influence on largemouth bass behavior are poorly understood.

Largemouth bass have been collected in salinities as high as 24 parts per thousand (ppt) (Bailey et al. 1954) and are commonly

collected in Louisiana marshes in salinities up to 12 ppt (personal observation). However, Renfro (1959) reported that salinities above 9 ppt appeared to be chronically lethal. Similar findings were reported by Tebo and McCoy (1964), who suggested that largemouth bass preferred salinities of less than 4 ppt. Salinity has been reported to influence the seasonal abundance of Louisiana marsh bass populations, with marsh bass most abundant in spring and early summer when salinities are low (Carver 1966). Bulkley (1975) stated that largemouth bass should not be expected to maintain normal populations in waters in which they are continually exposed to more than 3.5 ppt salinity.

It is important from both a biological and management standpoint to determine the impacts of salinity fluctuations on marsh bass habitat use, as well as the physiological adaptability of largemouth bass to high salinity waters. Knowledge of largemouth bass adaptations to brackish waters would contribute not only to our understanding of largemouth bass biology, but would also provide information for development of future management plans involving coastal largemouth bass populations. These data could be particularly important in view of the current problems of salinity intrusion into coastal marshes and proposed water management programs that significantly alter seasonal locations of fresh-saltwater mixing zones (Gosselink et al. 1979, Herke 1979).

CHAPTER 2. STUDY AREA

The study area was a brackish marsh located in Lafourche Parish, Louisiana (Fig. 2.1). The marsh contained a network of navigation canals dredged in the late 1940's for oil and gas exploration. These canals were approximately 1 m in depth and 40 m in width. Spartina patens was the predominant species of shoreline vegetation which also included goldenrod (Solidago sempervirens) and bulltongue (Sagittaria lancifolia). Submergent coontail (Ceratophyllum demersum) was present when salinities were less than 1 ppt.

Tidal cycles in the marsh were diurnal with a tidal range averaging 0.5 m. In winter, north winds pushed water out of the marsh decreasing salinities. However, south winds during summer pushed waters from the Gulf of Mexico into the marsh, increasing salinities. During south winds and low rainfall, saltwater intrusion was extensive. Salinities in the study area ranged from 0-12 ppt from January to December, but were typically 3-4 ppt for most of the year. Surface water temperatures ranged from 10 to 32^{o}C. Thirty-one fishes were collected from the study area (Table 2.1).

Collections were also made at two freshwater study sites: Ben Hur Lake, a 6.9-ha lake on Louisiana State University's (LSU) Ben Hur Research Farm, and False River, an 860-ha oxbow lake of the Mississippi River.

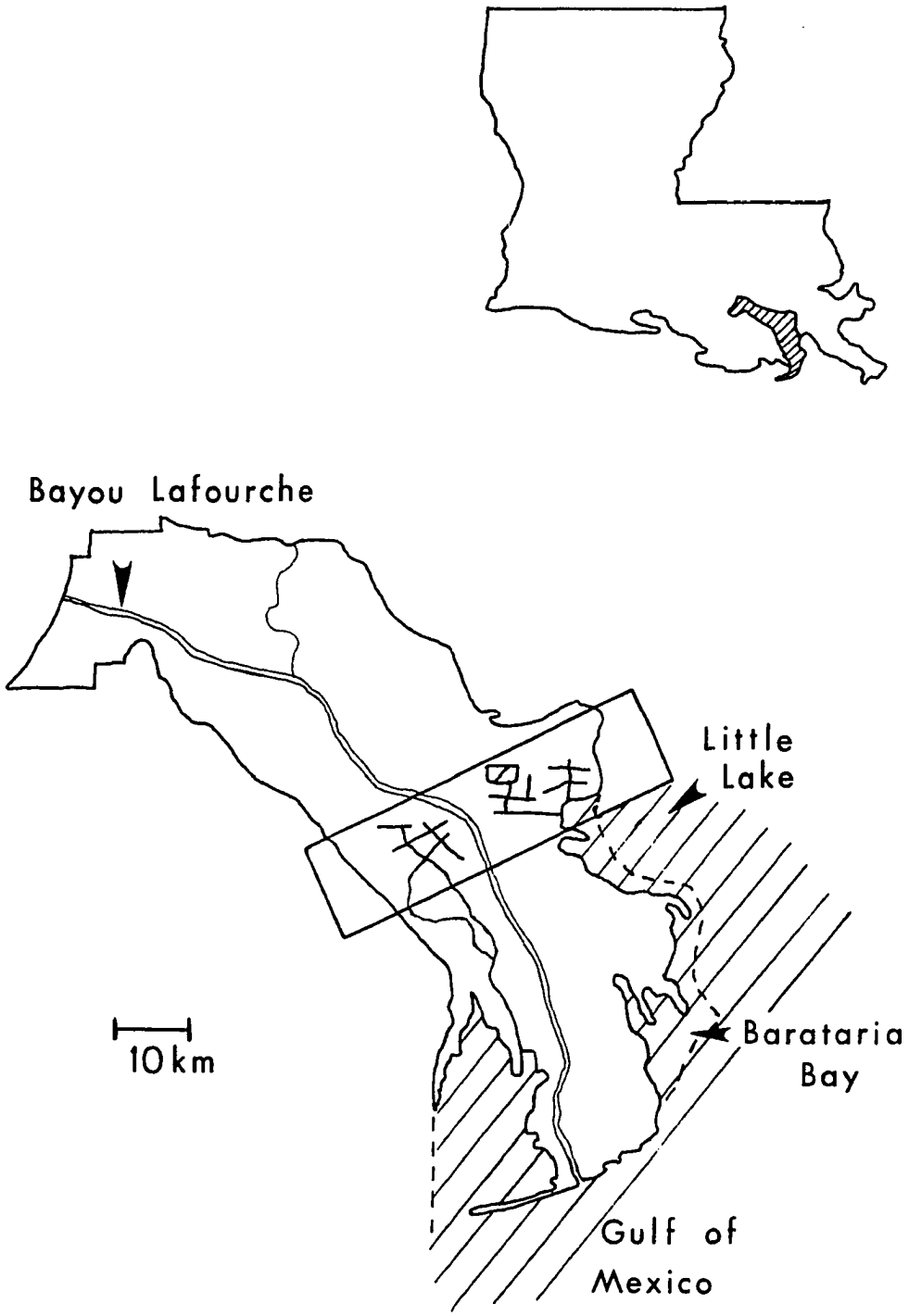

Figure 2.1. Location of the study area (inset) in Lafourche Parish, Louisiana.

Table 2.1. List of fish taxa collected from a brackish marsh in southcentral Louisiana from January to December 1986.

Common Name	Scientific Name
alligator gar	*Lepisosteus spatula*
longnose gar	*Lepisosteus osseus*
spotted gar	*Lepisosteus oculatus*
ladyfish	*Elops saurus*
American eel	*Anguilla rostrata*
Gulf menhaden	*Brevoortia patronus*
channel catfish	*Ictalurus punctatus*
hardhead catfish	*Arius felis*
Atlantic needlefish	*Strongylura marina*
Gulf killifish	*Fundulus grandis*
mosquitofish	*Gambusia affinis*
sailfin molly	*Poecilia latipinna*
pipefish	*Syngnathus* sp.
yellow bass	*Morone mississippiensis*
largemouth bass	*Micropterus salmoides*
warmouth	*Lepomis gulosus*
redear sunfish	*Lepomis microlophus*
bluegill	*Lepomis macrochirus*
spotted sunfish	*Lepomis punctatus*
hybrid sunfish	*Lepomis* spp.
Crevalle jack	*Caranx hippos*

Table 2.1. (cont.)

Common Name	Scientific Name
pinfish	*Lagodon rhomboides*
sheepshead	*Archosargus probatochephalus*
redfish	*Sciaenops ocellatus*
spotted seatrout	*Cynoscion nebulosus*
croaker	*Micropogonias undulatus*
spot	*Leiostomus xanthurus*
striped mullet	*Mugil chephalus*
goby	Gobiidae
southern flounder	*Paralichthys lethostigma*
Atlantic stingray	*Dasyatis sabina*

CHAPTER 3. GROWTH OF LARGEMOUTH BASS IN LOW-SALINITY ENVIRONMENTS

ABSTRACT

Age and growth data were evaluated for largemouth bass inhabiting a brackish marsh and a freshwater lake in southcentral Louisiana. Marsh bass were small compared to freshwater bass, although growth rates of older fish equaled or exceeded those of freshwater fish. Relative weight of marsh bass indicated excellent condition during all seasons, while freshwater fish exhibited reduced condition in early spring and fall. Small size and slow growth rate of marsh bass relative to freshwater populations have been reported from other Gulf and mid-Atlantic areas of the U.S. Laboratory trials consisting of 120-day exposure of marsh and freshwater largemouth bass to four salinity levels (0, 4, 8, and 12 ppt) indicated no significant differences ($P>0.05$) in specific growth rate of marsh bass held at 0, 4, and 8 ppt salinity. Similarly, no significant differences ($P>0.05$) were detected in specific growth rate of freshwater largemouth bass exposed to 0 and 4 ppt. However, growth of freshwater largemouth bass held at 8 ppt was significantly lower than growth at 0 ppt. All fish held at 12 ppt stopped feeding within weeks after the experiment began and died before the experiment ended.

Sheared principal components analysis indicated differences in body shape between marsh and freshwater largemouth bass. Characteristic body morphology and growth of marsh bass suggest an adaptation to abiotic and biotic conditions inherent in low-salinity environments. Increased osmoregulatory efficiency of small individuals combined with predator-mediated impacts on foraging habitat use may be primary factors influencing observed growth patterns.

INTRODUCTION

Largemouth bass in brackish habitats are reported to be small with slow average growth rates (Herring 1981). A creel census conducted in Alabama's Mobile River Delta indicated that the average marsh largemouth bass taken by anglers in 1980 weighed 390 grams (Tucker 1985). Anglers rarely harvested marsh largemouth bass in excess of 2.3 kg. Electrophoretic analysis of largemouth bass in Alabama did not detect genetic differences between brackish and freshwater populations (Hallerman et al. 1986) and these authors suggested that slow growth and small size of marsh largemouth bass were probably due to environmental factors.

Of obvious importance to brackish marsh physicochemistry are periodic fluctuations in salinity, which are usually caused by tidal or wind-driven influxes of high-salinity seawater, or storm-related influxes of freshwater. In this study, I examine age, growth, and condition of largemouth bass from a Louisiana brackish marsh and evaluate the effect of salinity on largemouth bass growth patterns.

METHODS

Age and Growth

Field Studies.-Largemouth bass were collected from the marsh and False River by castnetting, angling, and electroshocking. In the laboratory, total length (TL; mm) and weight (g) were recorded and sex was determined by dissection. Relative weight (W_r, Wege and Anderson 1978) was used to evaluate condition and was calculated as described by Anderson and Gutreuter (1983). Otoliths (sagittae) were removed and sectioned transversely in the dorsoventral plane (Hoyer et al. 1985). Each otolith was sanded from the posterior end to near the nucleus with coarse sandpaper and cemented to a microscope slide. The anterior side was then sanded as close to the nucleus as possible with fine sandpaper. Sectioned otoliths were etched with 0.1N HCl and viewed in transmitted light under a stereomicroscope fitted with an ocular micrometer. Otolith radius (OR) and annuli were measured from the nucleus to the proximal edge, just ventral to the central groove. Hyaline bands were considered to be annuli (Taubert and Tranquilli 1982). Total lengths-at-age were back-calculated using the Lee model (Carlander 1981) transformed by $\log_e$. Instantaneous rates of growth were estimated using backcalculated lengths-at-age for each fish in the formula $\log_e(l_{t+1}) - \log_e(l_t)$, where t=age in years. To calculate growth rates of age I fish, a length of 3 mm was used for t=0.

Stomachs were excised and preserved in 10% formalin for food habit analysis. Identification and enumeration of stomach contents were conducted with a stereomicroscope. Food items were identified to the lowest taxon possible, and the volume of items of each taxon in each

stomach determined by water displacement. Food items were weighed (wet weight) and then dried at 105°C for 24 hours to determine dry weight.

Laboratory Studies.-Laboratory trials were conducted to evaluate the effect of salinity on growth of marsh and freshwater largemouth bass. Twenty-four largemouth bass (185-318 mm) were collected from each of the two sites, the marsh and Ben Hur Lake, and transported to laboratory facilities at LSU, where total length and weight were recorded. Fish were held individually in 38-L aerated tanks for a two-week acclimation period before experiments began.

Four salinity concentrations (0, 4, 8, and 12 ppt) with six fish from each location per salinity, were established by use of Instant Ocean sea salt. Salinity was increased 1 ppt per day until final concentrations were reached. A YSI Model 33 salinometer (Yellow Springs Instrument Co., Yellow Springs, Ohio) was used to monitor salinity. All fish were fed live golden shiners (Notemigonus crysoleucas) at a rate of about 2% body weight per day. Tanks were maintained at a constant water temperature of 22°C and a 12-hour photoperiod. An undergravel filtration system was used and about one-quarter of the tank's water volume was replaced every month. Nitrite and ammonia concentrations were monitored using a Fisher Model 750 Accumet selective ion analyzer and were less than 0.1 mg/l. Dissolved oxygen was measured using a YSI Model 55B oxygen meter and averaged 7.5 ppm (85% saturation).

Laboratory trials evaluated growth for a 120 days. Upon termination of the experiment or death of individual fish, total length, and weight

of each fish were recorded. Dead fish were taken immediately to the LSU School of Veterinary Medicine, Aquatic Animal Disease Project, for pathological examination.

A relative specific growth rate (G) was used to evaluate growth during laboratory experiments and was calculated using the formula:

$$G = \frac{\log_e \text{final weight} - \log_e \text{initial weight}}{\log_e \text{initial weight}} \text{ -- time (days)}$$

Morphometric Analysis

Thirty-five fish collected from each of the two sites, the marsh and False River, were transported to the laboratory and anesthetized with MS-222. Ten morphometric variables (Table 3.1) were measured (mm) with electronic calipers on the left side of each fish.

Statistical Analysis

All data were analyzed using SAS (SAS Institute Inc. 1985). Age and growth data were analyzed using the general linear model procedure. Morphometric variation was analyzed using sheared principal components analysis to discriminate shape among groups that vary in size (Bookstein et al. 1985). Morphometric data were log transformed to reduce correlation of measurement means and variances. Statistical significance was declared at the $P<0.05$ level.

Table 3.1. List of ten morphometric variables recorded for largemouth bass from False River and Lafourche Parish, Louisiana.

Morphometric Character
1). Total length
2). Snout-dorsal fin origin length
3). Dorsal fin base length
4). Caudal peduncle depth
5). Anal fin base length
6). Pelvic fin origin-anal fin origin length
7). Snout-pelvic fin origin length
8). Body depth to pelvic fin origin
9). Body depth to anal fin origin
10). Shoulder width at dorsal fin origin

RESULTS

A total of 133 largemouth bass was collected from the marsh between January and December 1986 in salinities ranging up to 12 ppt. Marsh bass ranged from 92 to 366 mm TL (mean=260 mm $\pm$ 4.0 SE) and 11 to 871 g (mean=281 g $\pm$ 13.2 SE) in weight. Fish that were 200-250 mm in length were numerically dominant (50%). Freshwater largemouth bass from False River (N=115) ranged from 152 to 485 mm TL (mean=306 mm $\pm$ 5.0 SE) and 46 to 1785 g (mean=431 g $\pm$ 21.8 SE).

Of the 83 marsh bass stomachs examined, 34% were empty (Table 3.2). Paleomonetes sp. was the most abundant food item, representing 29.3% of all food items consumed. Fishes, primarily Fundulus grandis, were the most frequently occurring item and were also the most important prey item by percent weight. Brown shrimp (Penaeus aztecus), was the most important single item by percent weight.

Length-weight, condition

No differences in the length-weight relationship among sexes or ages were detected and therefore data were pooled:

$$\log_e(\text{weight}) = -11.39 + 3.04 \log_e(\text{length}) \quad (r^2=0.98) \quad \text{Marsh}$$

$$\log_e(\text{weight}) = -11.72 + 3.08 \log_e(\text{length}) \quad (r^2=0.98) \quad \text{Freshwater.}$$

The slope of the length-weight relationships for marsh and freshwater largemouth bass were not different.

Relative weight of marsh bass ranged from 82.6 to 151.8 with a mean of 102.2 $\pm$ 0.9 SE. No differences in mean monthly W_r values from January through December were detected. Mean W_r of largemouth bass from False River was 95.5 $\pm$ 0.9 SE, with June W_r (mean=102.1) significantly higher than January (93.9), March (96.5), and October (92.1). Mean W_r of False River largemouth bass was lower than the mean value of marsh bass.

Table 3.2. Food habits of largemouth bass collected from a brackish marsh in southcentral Louisiana from January to December 1986. (vol=volume in mm, wt=weight in g).

Taxon	Number	% by number	Frequency of Occurrence	% by vol	% by wet wt	% by dry wt
Crustacea	77	49.0	33.3	37.3	36.8	43.3
Amphipoda	1	0.6	2.1	0.5	0.3	0.4
Decapoda						
Paleomonetes sp.	46	29.3	12.5	11.6	12.4	10.7
Penaeus aztecus	27	17.2	12.5	22.7	21.5	28.6
Callinectes sapidus	1	0.6	2.1	0.3	0.4	0.2
Uca sp.	2	1.3	4.2	2.1	2.2	3.5
Insecta						
Odonata	5	3.2	10.4	0.6	0.5	0.5
Osteichthyes	75	47.8	70.8	61.8	62.8	56.8
Fundulus grandis	16	10.2	16.7	13.6	13.8	11.3
Menidia sp.	27	17.2	6.3	11.4	14.1	11.9
Brevoortia patronus	7	4.5	10.4	17.9	14.1	15.9
unid. fish	25	15.9	37.5	18.9	20.8	17.0
Total	157					

Number of stomachs examined-- 83

Number of stomachs with food-- 55 (66%)

Comparison of mean W_r values for those months in which both populations were sampled (N=4) revealed that marsh bass had higher W_r values in March and June.

Age and Growth

Laboratory.-No differences were detected among specific growth rates of marsh bass held at 0, 4, and 8 ppt salinity during laboratory growth trials (Table 3.3), nor in specific growth rate of Ben Hur Lake freshwater largemouth bass exposed to 0 and 4 ppt. However, specific growth rate of freshwater largemouth bass held at 8 ppt was lower than at 0 ppt. All largemouth bass held at 12 ppt stopped feeding within one week after the experiment began and died before the experiment ended. Pathological examination revealed that death was not the result of bacterial infestation or chemical toxicity. Two largemouth bass held at 8 ppt died before the experiment ended due to low dissolved oxygen concentrations when mechanical aeration failed.

Field.-Largemouth bass collected from the marsh study area and False River ranged from ages I to IV and I to V, respectively. Within sampling location, length and otolith measurements were pooled for males and females as no differences were detected between sexes for the TL:OR relationship:

$$\log_e(TL) = 2.26 + 0.47\log_e(OR) \quad (N=74, r^2=0.87) \quad \text{Marsh}$$

$$\log_e(TL) = 2.79 + 0.73\log_e(OR) \quad (N=53, r^2=0.81) \quad \text{Freshwater.}$$

Based on back-calculated total lengths-at-age, marsh bass averaged 146 mm at age I (Table 3.4), while False River fish averaged 161 mm at age I (Table 3.5).

Table 3.3. Mean relative specific growth rates for largemouth bass from Ben Hur Lake and a brackish Louisiana marsh exposed to four salinity levels (N=6 per salinity for each location). Means with the same letter are not significantly different. No significant differences were detected between locations. (Values have been multiplied by 10^4 for clarity; numbers in parenthesis indicate standard deviation).

Salinity (ppt)	Location				
	Ben Hur Lake			Brackish Marsh	
0	7.61 (3.5)	A		4.29 (4.1)	A
4	4.34 (3.4)	A	B	3.00 (1.8)	A
8	2.58 (1.5)		B	2.82 (1.1)	A
12	-7.40 (5.1)	C		-3.93 (3.2)	B

Table 3.4. Calculated total lengths-at-age (mm) for largemouth bass collected from a brackish marsh in Lafourche Parish, Louisiana.

Age at Capture	Number of Fish	Mean Calculated Total Length at Annulus I	II	III	IV
I	5	158	-	-	-
II	43	143	218	-	-
III	22	140	214	280	-
IV	4	142	207	273	321
mean calculated total length (unweighted)		146	213	277	321
mean calculated annual growth increment (unweighted)		146	67	64	44
range of calculated total lengths-at-annulus		118-191	182-255	233-300	292-340

Table 3.5. Calculated total lengths-at-age (mm) for largemouth bass collected from False River, Louisiana.

Age at Capture	Number of Fish	Mean Calculated Total Length at Annulus I	II	III	IV	V
I	5	178	-	-	-	-
II	22	149	259	-	-	-
III	17	168	282	319	-	-
IV	4	160	259	318	370	-
V	3	148	283	340	367	393
mean calculated total length (unweighted)		161	271	326	369	393
mean calculated annual growth increment (unweighted)		161	110	55	43	24
range of calculated total lengths-at-annulus		121-208	215-318	275-369	342-394	368-419

The shorter length-at-age of marsh bass relative to freshwater fish was most evident between ages I and II, with a difference in mean annual length increment of 43 mm. Instantaneous growth rates of marsh bass were lower than those of freshwater largemouth bass during the first and second years of life (Table 3.6). However, marsh bass growth rates exceeded those of freshwater fish during year three and no differences in growth rates were noted for year four; although, sample sizes of age-IV fish were small.

Morphometric Analysis

Sheared principal components analysis of morphometric data revealed that 96.4% of the total variance was explained along the first two axes (Table 3.7). Component loadings were approximately equal on principal component I, which was considered a measure of general size (Winans 1985). Sheared principal component II (SPCII), a size-free shape component, was considered an indicator of body shape. Marsh bass exhibited lower SPCII values (shorter dorsal and anal fin bases, deeper caudal peduncle and longer abdominal length) while freshwater largemouth bass exhibited higher SPCII values (Figure 3.1).

Table 3.6. Instantaneous growth rates (IGR) of largemouth bass from a freshwater lake and brackish marsh. Only data for ages I to IV were examined. (N=number of individuals; numbers in parenthesis indicate standard deviation).

		AGE			
	Location	I	II	III	IV
IGR	Freshwater	3.97 (0.12)	0.51 (0.10)	0.17 (0.03)	0.14 (0.04)
	Marsh	3.87 (0.11)	0.41 (0.06)	0.26 (0.05)	0.17 (0.03)
N	Freshwater	43	43	21	4
	Marsh	69	69	26	4

Table 3.7. Variable coefficients on principal component I (PCI) and sheared principal component II (SPCII) from an analysis of 10 morphometric characters for marsh and freshwater largemouth bass. Blanks indicate coefficients with an absolute value of less than 0.2.

Morphometric Character	PCI	SPCII
Total length	-0.293	
Snout-dorsal fin origin length	-0.301	
Dorsal fin base length	-0.316	0.200
Caudal peduncle depth	-0.329	-0.458
Anal fin base length	-0.270	0.762
Pelvic fin origin-anal fin origin length	-0.306	-0.275
Snout-pelvic fin origin length	-0.311	
Body depth to pelvic fin origin	-0.334	
Body depth to anal fin origin	-0.326	
Shoulder width at dorsal fin origin	-0.366	
% of Total Variance	91.6	4.8

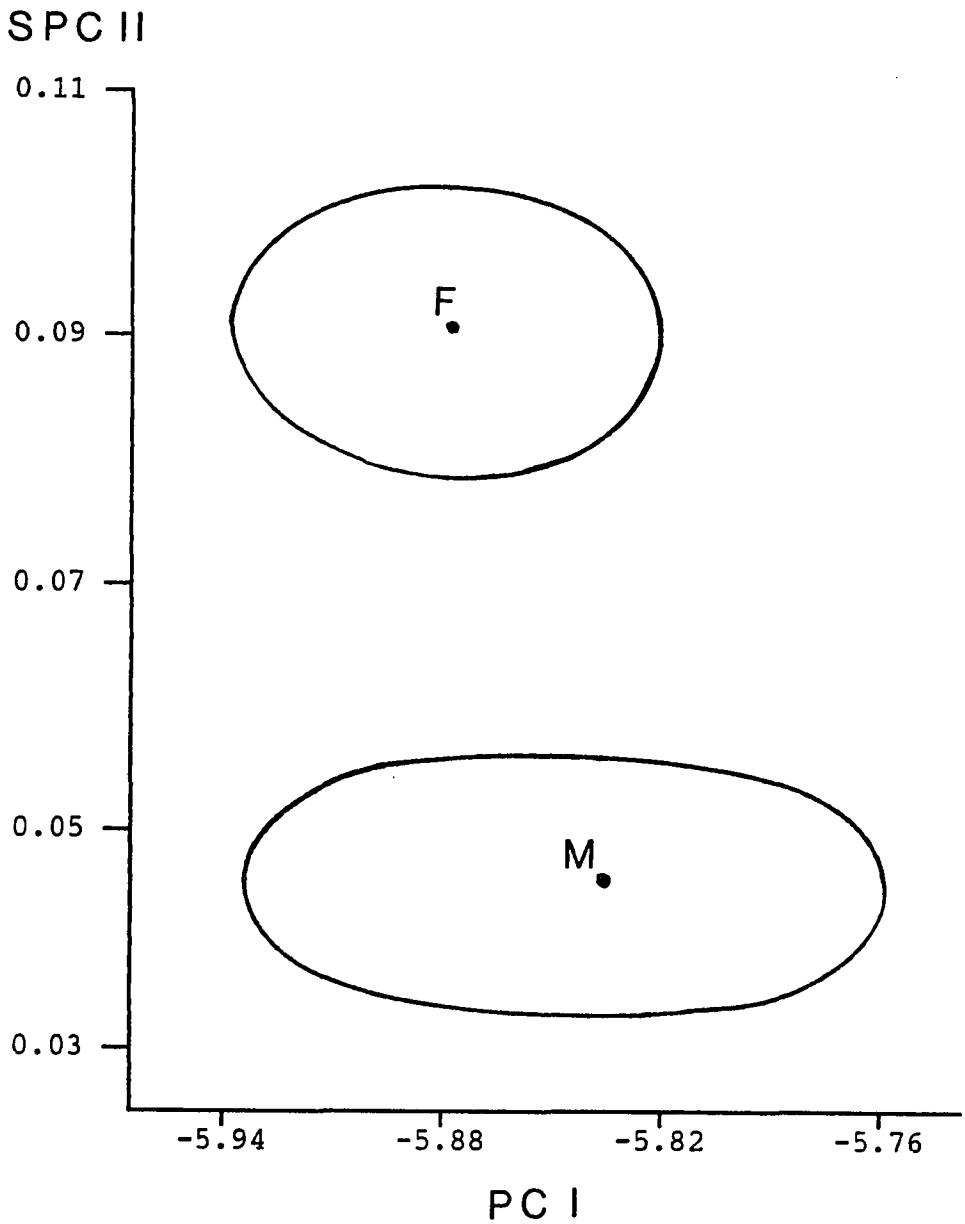

Figure 3.1. 95% confidence ellipses for bivariate means of sheared principal component II (SPC II) and principal component I (PC I) from an analysis of 10 morphometric characteristics of marsh and freshwater largemouth bass. Points represent centroid means (F=False River, M=coastal marsh).

DISCUSSION

Lengths-at-age of largemouth bass from the marsh study area were similar to those reported for other coastal largemouth bass populations along the Gulf (Table 3.8). Differences in length-at-age between marsh and freshwater largemouth bass were consistent with previously published growth studies and suggest an alternative growth pattern for largemouth bass inhabiting low-salinity environments. A similar pattern of reduced marsh bass length-at-age relative to that of freshwater largemouth bass was evident for populations along the east coast of the U.S.; although, length differences between marsh and freshwater populations were of lesser magnitude (Table 3.9).

That observed growth patterns of marsh bass were a result of redistribution of somatic growth relative to freshwater fish, rather than the result of some other phenomenon such as growth-related differential mortality, was evidenced by differences in body morphology between the two populations. Marsh bass have been described as having a short, rotund body (Tucker 1985, Hallerman et al. 1986), and length-weight regressions indicated that marsh bass were slightly heavier than freshwater fish of similar length. Multivariate analyses of selected morphological measurements revealed that relative to freshwater fish, marsh bass were characterized by a deeper peduncle, shorter fins, and a longer abdominal length. Although these measurements do not reveal specifically how growth characteristics of marsh and freshwater largemouth bass differ, they do indicate allometric differences between the two populations.

Several explanations have been advanced to explain why largemouth bass inhabiting low-salinity habitats exhibit reduced length-at-age

Table 3.8. Calculated total lengths-at-age (mm) for largemouth bass from various freshwater and coastal locations along the Gulf of Mexico coast (only data for ages I to V were examined).

Location	Age I	II	III	IV	V
Freshwater					
present study-False River	161	271	326	369	393
Old River, LA[1]	203	304	363	414	454
Darbonne Pit, LA[2]	168	246	302	345	368
Lewis Smith Reservior, AL[3]	147	274	358	401	442
Grenada Reservior, MS[3]	155	279	338	381	437
Idlewild Lake, LA[4]	218	267	287	351	388
Louisiana[4]	193	287	368	478	531
unweighted mean[4] (AL,GA,LA,TX)	160	256	315	391	418
Mean	177	273	332	392	432
Coastal					
present study-Louisiana marsh	146	213	277	321	-
Big Burn, LA[1]	109	193	256	314	379
Mobile Delta, AL[5]	145	229	291	351	397
Jackson County, MS[6]	138	212	267	314	388
Harrison County, MS[6]	136	213	260	305	375
Hancock County, MS[6]	149	221	265	322	379
Mean	137	214	268	321	384

[1]Colle et al. 1976
[2]Shay and Ward 1969
[3]Webb and Reeves 1975
[4]Carlander 1977
[5]Tucker 1985
[6]Lorio et al. 1982

Table 3.9. Calculated total lengths-at-age (mm) for largemouth bass from various freshwater and coastal locations along the mid-Atlantic coast (only data for ages I to V were examined).

Location	Age I	II	III	IV	V
Freshwater[1]					
Claytor Lake, VA	142	274	356	404	429
Falls Lake, NC	122	241	351	414	455
Hiwassee Reservior, NC	144	259	328	374	424
Badin Lake, NC	130	246	361	429	465
James Lake, NC	145	241	396	452	-
Snowden Pond, MD	180	287	343	-	-
Rhodhiss Lake, NC	124	206	290	376	450
Kerr Lake, NC	178	279	348	401	442
unweighted mean (DE,MD,NC,VA)	133	235	312	374	424
Mean	144	252	343	403	441
Coastal					
Pasquotank River, NC[2]	136	223	296	352	392
Chowan River, NC[2]	123	215	277	300	369
Tar-Pamlico River, NC[2]	121	217	298	362	398
Maryland Coastal Plain[3]	124	246	330	389	429
Chesapeake Bay, MD[3]	149	257	331	378	419
Nanticoke River, DE[3]	152	268	336	386	422
Mean	134	238	311	361	405

[1]Carlander 1977

[2]Guier et al. 1978

[3]Fewlass 1980

relative to freshwater fish. Swingle and Bland (1974) suggested that as salinity increased in late spring, older marsh bass (Age I and above) moved to freshwater areas already occupied by freshwater largemouth bass populations, resulting in overcrowding and reduced growth. A similar conclusion was reached by Tucker (1985) based on reduced condition of marsh bass under 240 mm TL. Seasonal absence of older marsh bass from the study area during periods of elevated salinity was also noted in the present study, but reduced growth was already evident in marsh bass by age I, and growth rates of older marsh bass actually exceeded those of freshwater fish. In addition, marsh bass exhibited uniformly high condition, as previously reported for marsh bass inhabiting the Mobile River Delta (Hallerman et al. 1986), which would not be expected under crowded, forage-limited conditions.

Lorio et al. (1982) indicated that small size and slow growth of marsh bass in three coastal river-marsh systems of Mississippi were influenced by diet quality. These authors felt that the marsh forage base was dominated by small invertebrates that provided inadequate net energy to sustain maximum growth. Growth depensation in young largemouth bass has been reported to be a function of prey type (Keast and Eadie 1985). Keast and Eadie (1985) noted that within an age class, larger largemouth bass obtained a higher energy content per mg of prey in their diet than did smaller fish. This difference was attributed to a higher proportion of fish in the diet of larger individuals. However, while diet quality of smaller largemouth bass was lower, condition was equal to or higher than that of larger fish.

While adult freshwater largemouth bass feed primarily on fish (Carlander 1977), dietary proportions of fish in adult Gulf marsh bass are typically less than 50% by number, ranging from 5.7-47.8% (Lorio et al. 1982, present study). Although fish prey are abundant in marsh areas, they may not be available to foraging marsh bass. The majority of marsh bass were found in shallow water among dense submerged macrophyte beds, where foraging efficiency is low (Savino and Stein 1982, Anderson 1984). While perhaps not providing a favorable foraging habitat, macrophyte beds in the present study area provided protection for marsh bass from large predators that were common in the study area. Predator modification of prey foraging behavior has been documented for a number of fishes (Mittelbach 1981, 1984, Kneib 1987, Schlosser 1987, Holbrook and Schmitt 1988). Doerzbacher (1980) suggested that the presence of large predators contributed to confinement of largemouth bass to nearshore regions of freshwater canals in Louisiana. Alligators (Alligator mississippiensis) and alligator gar (Lepisosteus spatula) were commonly found in the study area, and approximately 40% of the marsh bass that were collected had open wounds or scars. Unlike the trophic position of largemouth bass in many warmwater ponds or reserviors, Louisiana marsh bass occupy an intermediate rather than top trophic level. In such habitats, predation risk may affect marsh bass growth rates by influencing marsh bass habitat selection and foraging profitability, similar to interactions reported among other centrarchids (Mittelbach 1981, 1984). Interestingly, differences in length-at-age between Atlantic coast marsh and freshwater largemouth bass populations

are of lesser magnitude and diets of Atlantic coast marsh bass appear to closely reflect the diet of freshwater largemouth bass (Mullis and Davies 1977).

On the basis of limited electrophoretic differences between marsh and freshwater largemouth bass, Hallerman et al. (1986) concluded that environmental factors were responsible for observed marsh bass growth patterns. Coastal marshes along the Atlantic and Gulf coasts are subject to periodic influxes of saltwater, and it was evident from laboratory experiments in the present study that largemouth bass populations from freshwater differed from that of the marsh in growth response to increasing salinity. Marsh bass exhibited reduced growth relative to freshwater bass at 0 ppt, indicating a lower growth potential. However, reductions in marsh bass growth with increasing salinity were negligible compared to those of freshwater fish, particularly at 8 ppt, indicating physiological exaptation (Gould and Vrba 1982) of marsh bass to low-salinity conditions.

If marsh bass growth patterns are a response to elevated or rapidly-fluctuating salinity, greater physiological efficiency of smaller marsh bass could result in the observed trends in lengths-at-age. In teleost fishes, the ratio of gill surface area per unit body weight is inversely related to body weight (Muir and Hughes 1969), perhaps resulting in an osmoregulatory advantage for smaller fish. However, in many coastal marshes salinities do not exceed 3 ppt throughout the year, yet resident largemouth bass still exhibit reduced length-at-age (Colle et al. 1976). In addition to variable salinity, marshes are typically

characterized by high summer water temperatures and low dissolved oxygen concentrations. In the present study, marsh water temperatures as high as 32°C and mid-morning dissolved oxygen concentrations as low as 3 ppm were common in summer. Murphy and Houston (1974) found evidence for increased Na^+-K^+ ATPase activity at high water temperatures in smaller goldfish (Carassius auratus) as compared to larger individuals; although, results were not conclusive. If such relationships hold for largemouth bass, smaller individuals might be better able to cope with all aspects of marsh physicochemistry than larger fish.

Although, selection pressures vary among coastal habitats along the Atlantic and Gulf coasts, small size and slow growth are characteristic of marsh bass throughout their range. The specific causes of marsh bass growth patterns relative to those of freshwater largemouth bass are still undetermined, and probably a complex interaction of several factors, including fluctuating salinity, prey availability, habitat complexity, and predation risk are responsible. Based on length-at-age, these factors influence Gulf marsh bass growth before age I, whereas reduced length-at-age of Atlantic marsh bass does not become apparent until Age III or IV.

Previous hypotheses have implied that marsh bass are stressed by physicochemical conditions inherent in marsh systems. Such an assumption is not supported by marsh bass condition factors, which are typically high (Hallerman et al. 1986). In our study, high relative weights of marsh bass throughout the year indicated an environment conducive to excellent growth (Anderson and Gutreuter 1983). In this light, marsh

bass growth did not appear to be "poor", but merely different from that of their freshwater counterparts. Identification of the physicochemical and abiotic factors that select for this alternative growth strategy will require laboratory and field experiments designed to assess the relative impacts of chemical, structural, and energetic factors on growth, survival and condition of marsh bass.

CHAPTER 4. MOVEMENTS AND SITE SELECTION OF LARGEMOUTH BASS IN A BRACKISH MARSH

ABSTRACT

Ultrasonic transmitters were implanted in ten largemouth bass and fish were tracked in a low-salinity canal in Lafourche Parish, Louisiana during the spring and summer of 1986. No significant differences ($P>0.05$) were detected between linear distance moved and changes in temperature, depth, salinity, and dissolved oxygen between locations. Salinity did not influence short term (daily) movements although salinity increases during late summer may have induced large-scale seasonal movements. Though tagged fish could not be located after salinities reached 8 ppt, largemouth bass smaller than tagged individuals were collected in the study area. These results suggest mobile and sedentary segments of marsh largemouth bass populations. The presence of large predators combined with potentially stressful physicochemical conditions may influence movement and site selection by largemouth bass in low-salinity environments.

INTRODUCTION

Studies of the distribution and movements of largemouth bass have served to evaluate habitat utilization by this species (Moody 1960, Lewis and Flickinger 1967, Mesing and Wicker 1986). The use of radio and ultrasonic telemetry has enabled researchers to define daily movements, home range, and homing ability of largemouth bass (Chappel 1974, Winter 1977, Doerzbacher 1980). Though such studies have been conducted in freshwater habitats, no study has examined the movements of largemouth bass in a brackish environment. In this study, I investigate movements and site selection by largemouth bass in a brackish marsh in southcentral Louisiana.

METHODS

Individual fish were tracked using coded ultrasonic transmitters (model UCTT-82, Sonotronics, Tucson, Arizona), a Sonotronics USR-5 digital receiver and a DH-1 directional hydrophone. Transmitters were cylindrical, 16 mm in diameter by 60 mm long, and weighed 20 gm (8 gm in water). They operated at a frequency of 75 khz with a range of 1000 m in seawater and had a lifespan of at least 6 months at 20°C. Individual fish were identified by a four digit pulse code. Temperature and salinity were measured using a YSI Model 33 salinometer and dissolved oxygen was measured using a Model 51B oxygen meter.

Adult marsh bass were collected by castnetting and angling from a canal within the study area (Fig. 4.1), transported to the laboratory, and held in 95-L tanks until surgical implantation of transmitters. Initially, each bass was held for one week to recover from capture stress, but holding time was reduced as the fish showed no apparent ill effects from handling.

Total length (mm, TL) and weight (gm) of each fish were recorded. Transmitters were implanted according to the procedures of Hart and Summerfelt (1975) and each fish was sexed prior to suturing. Bass were returned to the canal 24 hours after surgery. Fish were released in the middle of the canal approximately 300 m apart.

During spring 1986, largemouth bass locations were determined every 6 hours for a 72-hour period after release on 26 March and biweekly thereafter. Bass tagged during summer were located once every two weeks after release. Wooden stakes with orange flagging placed along the shoreline were used as landmarks to triangulate position. Distances were measured with a tape measure and a rangematic distance finder (Ranging

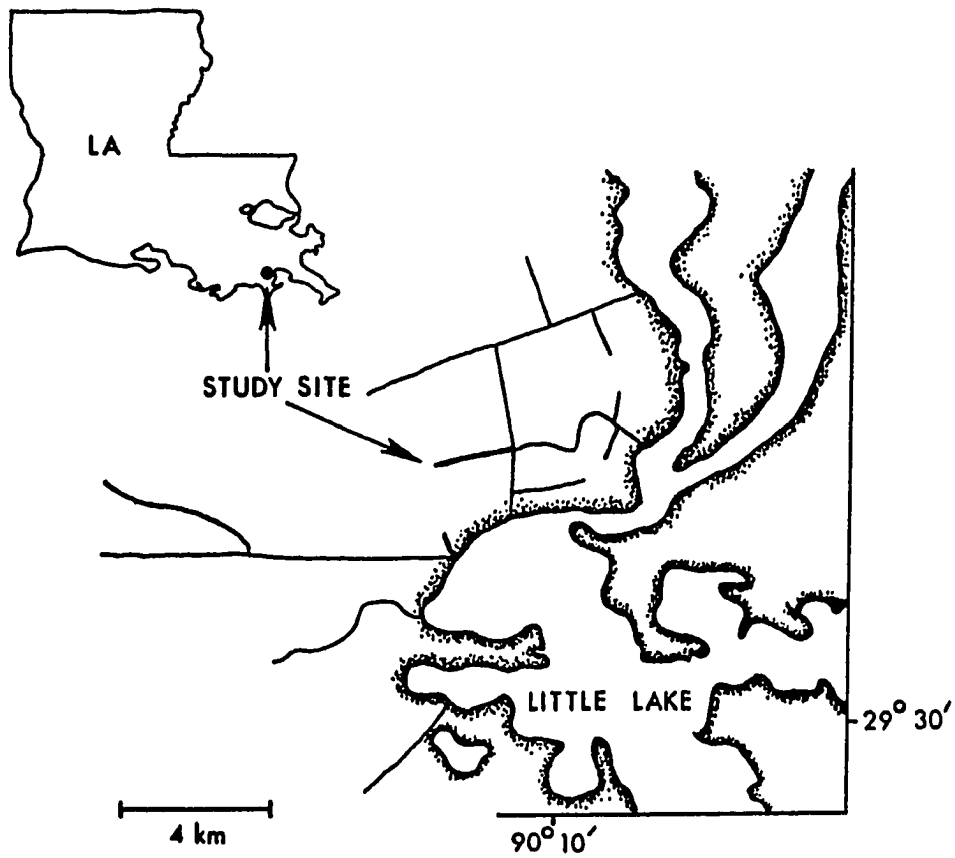

Figure 4.1. Location of the study site canal near Little Lake, Louisiana.

Inc., New York). As each fish was located, time of day, water depth, salinity, surface temperature, and surface dissolved oxygen were measured. During the spring tracking period, if a tagged bass had moved from its previous location, physicochemical parameters were also recorded at the previous location.

Locations were plotted on a Cartesian x-y coordinate system encompassing the area occupied by the fish. Home range size was determined using the maximum-area polygon method of Doerzbacher (1980). The shoreline was used as a boundary for home range estimates (Mesing and Wicker 1986). An observation-area curve (Odum and Kuenzler 1955) was constructed to determine if sufficient observations had been made to evaluate home range size. Odum and Kuenzler (1955) recommended that home range size be determined at the point on the curve beyond which each additional observation would produce less than a 1% increase in area. To determine what portion of the home range was actually used by the fish, a 'primary utilized area' was calculated (Doerzbacher 1980). Home range shape was described using an index of linearity determined by the ratio of maximum home range length to width (Ables 1969).

All data were analyzed using the general linear model procedure of SAS (SAS Institute Inc. 1985). Statistical significance was declared at the $P<0.05$ level.

RESULTS

External examination of transmitter-equipped largemouth bass held in the laboratory revealed that incisions healed within one week after surgery. These largemouth bass were observed actively feeding the day following surgery. Long-distance movements and erratic behavior by largemouth bass during the first week following transmitter implantation observed in other telemetry studies (Winter 1977, Mesing and Wicker 1986) was not evident in the present study. Therefore, tagged fish were assumed to have behaved normally.

Ten fish, 286-366 mm total length and 322.4-871.2 gm in weight were used in this study (Table 4.1). Six fish were tagged and released on 26 March. Although fish number 2228 was never located after release, the remaining five bass were located until 19 April. From 26 March-19 April, salinity ranged from 2-4 ppt and water temperature ranged from 18-27^{o}C. Dissolved oxygen concentrations ranged from 6.5-10.0 ppm. None of the tagged bass could be located on or after 3 May when salinity reached 8 ppt and water temperature was 26^{o}C.

Two bass were tagged and released on 31 July and two on 13 August. All four bass were tracked through 10 September. During this time, salinity ranged from 3-5 ppt and water temperature from 28 to 30^{o}C. Dissolved oxygen concentrations ranged from 3.0-12.1 ppm. None of the bass could be located on or after 27 September when the salinity reached 12 ppt and water temperature was 32^{o}C.

Tagged fish moved from the middle of the canal to the southern shoreline after release, but otherwise each fish remained near its release site and movements were generally parallel to the shoreline.

Table 4.1. Summary of telemetry data for 10 largemouth bass tagged with ultrasonic transmitters.

Fish	Total Length (mm)	Weight (gm)	Sex	Dates Active	Number of Fixes	Distance Moved (m)
2228	314	431.4	F	3/26/86	0	0
2264	307	405.8	F	3/26-4/19/86	10	425
2336	321	419.4	M	3/26-4/19/86	12	540
3227	306	418.7	M	3/26-4/19/86	12	556
2255	293	375.9	F	3/26-4/19/86	12	560
2327	326	496.6	F	3/26-4/19/86	10	381
2345	366	871.2	F	7/31-9/10/86	4	117
2363	318	464.5	M	7/31-9/10/86	4	230
2444	348	571.8	F	8/13-9/10/86	2	87
2354	286	322.4	M	8/13-9/10/86	2	65

Thirty of the 56 locations (54%) for the five bass tracked during the spring were observed within 5 meters of the southern shoreline (Fig. 4.2). During 26-29 March the average distance moved per day was 123.1 m. No differences were detected between distance moved and changes in water temperature, depth, salinity, dissolved oxygen among locations. Distance of each location from the shore was greater at night than during the day.

Distance moved and time of day were analyzed for the five bass tracked during 26-29 March. Time of day was classified into four daily time periods: dawn (0200-0800 hours), day (0800-1400 hours), dusk (1400-2000) and night (2000-0200 hours). Movement declined continuously from dawn to dusk and was less at night (Table 4.2).

A sufficient number of locations necessary to calculate home range size, as determined by observation-area analysis, was available for only two bass. Home range size for these bass was estimated at 0.22 and 0.12 ha and the primary utilized area was 0.06 and 0.008 ha, respectively (Figure 4.3). Linear index values were 5.48 and 9.23. Length of shoreline utilized was calculated for the five fish tracked during the spring and ranged from 161-261 m with a mean of 196.9 m. Length of shoreline used and total weight of fish were positively correlated (r=.77), however, length of shoreline and total length of fish were not (r=.44).

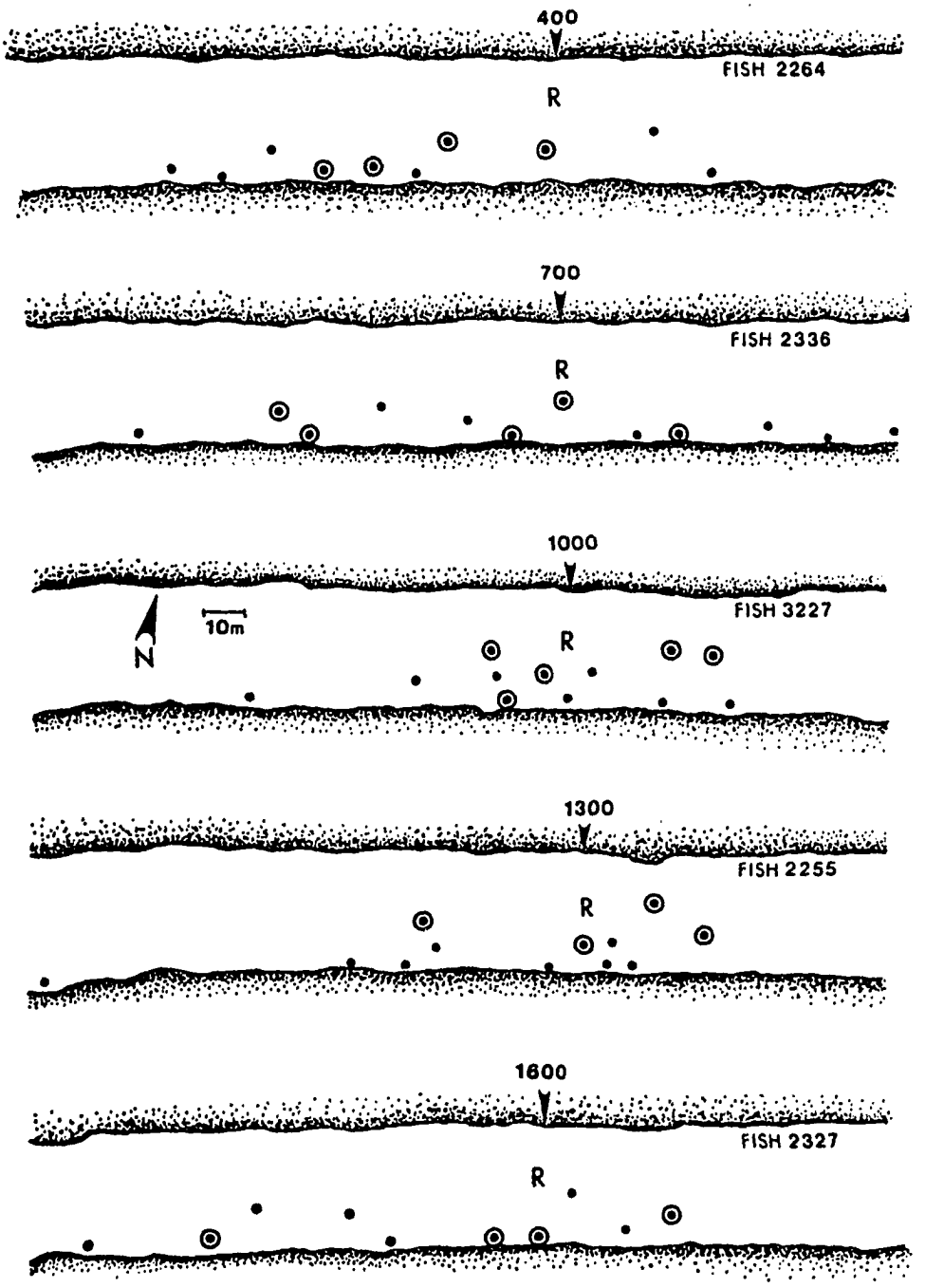

Figure 4.2. Locations of five largemouth bass tracked from 3/26-4/19/86 in the study site canal. R indicates release site and arrows indicate distance from the end of the canal in meters. Circled points indicate locations observed during the night.

Table 4.2. Mean distance moved for five bass tracked during 26-29 March 1986 during four daily time periods. Means with the same letter are not significantly different (P>0.05; numbers in parenthesis indicate standard error).

	Time (hours)	Mean Distance Moved (meters)			Number of Fixes
Dawn	(0200-0800)	61.2 (9.1)	A		14
Day	(0800-1400)	58.8 (5.8)	A		16
Dusk	(1400-2000)	45.3 (12.7)	A	B	11
Night	(2000-0200)	29.8 (5.0)		B	8

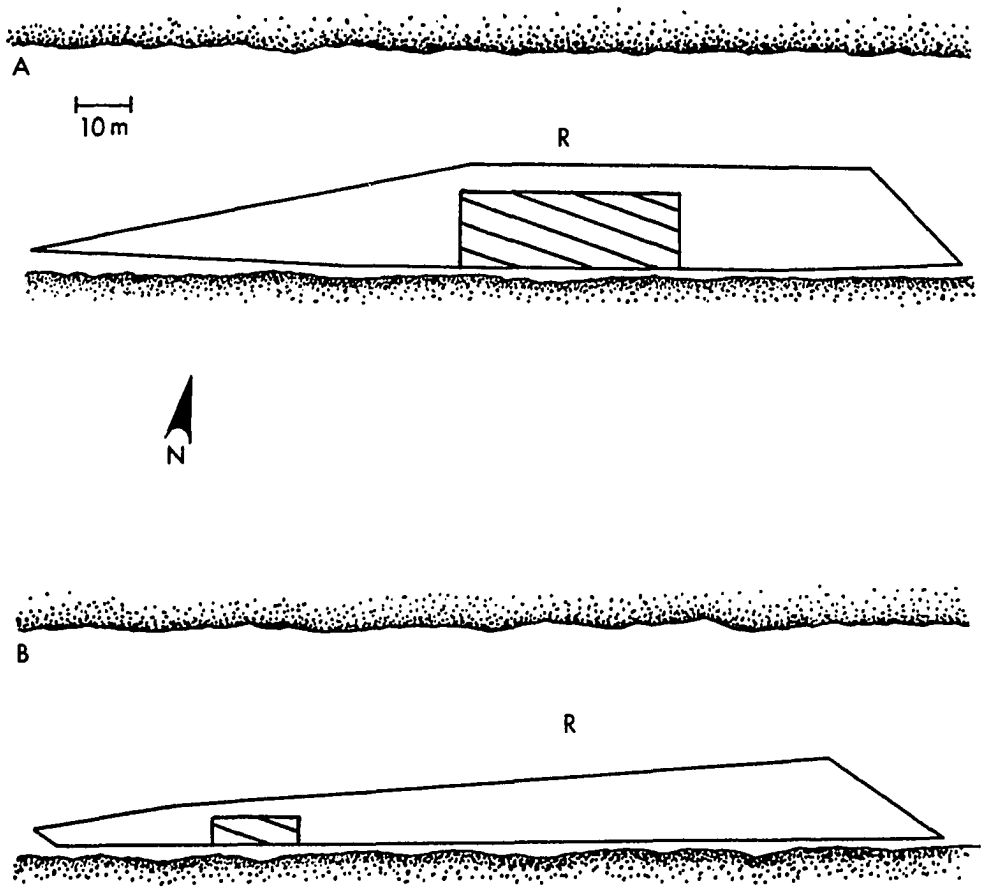

Figure 4.3. Home range of Bass #3227 (A) and Bass #2264 (B) in two sections of the study site canal. Convex polygon encloses maximum home range and shaded area represents primary utilized area. R indicates release site.

DISCUSSION

Home range has been defined as the area usually occupied by an animal (Hayne 1949). Restricted movements and home ranges of largemouth bass have been observed (Lewis and Flickinger 1967, Winter 1977, Neiman and Clady 1980, Doerzbacher 1980, Mesing and Wicker 1986), although the methods for determining home range have varied. Home range size in the present study was smaller than that observed by Winter (1977) for largemouth bass in a Minnesota lake, but was within the range of values observed for bass in canal systems in Louisiana and Florida (Doerzbacher 1980, Mesing and Wicker 1986) and comparable to home ranges reported for largemouth bass in an Oklahoma lake receiving thermal effluent (Neiman and Clady 1980). Primary utilized area and length of shoreline utilized was smaller than those observed by other investigators (Doerzbacher 1980, Mesing and Wicker 1986). A positive correlation between home range length (or length of shoreline utilized) and fish weight, similar to that of the current study, has been observed for other populations of largemouth bass (Chappel 1974).

Limited variation in water temperature, depth, salinity and dissolved oxygen observed in the canal during tracking periods made it difficult to evaluate physicochemical effects on marsh bass movement. Water movement in the shallow canal was relatively rapid as compared to that of open water areas of the marsh and therefore little stratification was observed. Variation in physicochemical parameters, and thus their influence on largemouth bass movement, was probably due to daily and seasonal factors such as rainfall and wind.

Although tagged fish could not be located after salinities increased to 8 ppt, other largemouth bass were still present in the canal. Largemouth bass ranging in size from 200 to 270 mm total length (smaller than tagged bass) were collected along the shoreline on 27 September at 12 ppt salinity and a water temperature of 32°C. When tagged bass could not be located within the canal, a search of the surrounding marsh was conducted, covering an area of approximately 8 km radius from the canal. Temperature, salinity, and dissolved oxygen appeared to be uniform throughout this area and the canal. Many sections of the surrounding marsh were inaccessible by boat and tagged fish could have moved into these areas and remained undetected. However, if tagged fish moved to avoid unfavorable physicochemical conditions, such movment would have had to cover distances greater than 8 km to avoid conditions similar to those found in the canal.

The existence of sedentary and mobile segments of bass populations has been suggested (Mesing and Wicker 1986). In an inventory study conducted by Swingle and Bland (1974) in Mobile Delta, Alabama, all age classes of largemouth bass were present in the lower delta and upper bay regions during winter and spring, but as salinity increased in summer and fall, only age 0 bass were present in these areas. The authors suggested that larger bass moved into less saline waters. Similar abundance patterns were noted in the present study. Although extensive movements of larger individuals could not be documented, largemouth bass populations in the marsh may be characterized by smaller resident fish and larger migratory individuals that move to areas of lower salinity

during the summer.

Movements of largemouth bass in the study canal appeared to consist of both short term (daily) and long term (seasonal) patterns. Short term salinity variation in the study canal was low and salinities were less than 4 ppt during most of the year. Therefore, the influence of salinity on daily movement patterns appeared to be minimal. Mesing and Wicker (1986), in a telemetry study of largemouth bass in a Florida lake-canal system, noted seasonal movements of bass during spawning directed toward canals and other areas which offered protection from wave action. Largemouth bass in coastal environments may seek canals and other protected areas as spawning sites. However, seasonally-high salinities may influence long-term movements and distribution of marsh bass.

The presence of young marsh bass in the study canal at salinities greater than 8 ppt indicated that factors other than salinity may have influenced observed movement and distribution patterns. Biotic interactions may be important determinants of daily and seasonal marsh bass movement. Doerzbacher (1980) suggested that potential predation from alligators (Alligator mississippiensis), alligator gar (Lepisosteus spatula) and other large predators may have contributed to confinement of largemouth bass to nearshore regions of freshwater canal systems in the Atchafalaya River basin, Louisiana. Predators such as alligators and alligator gar were commonly found in the study canal and many marsh bass collected displayed open wounds or scars. Movements of alligator gar appeared to be concentrated in the middle of the canal throughout its

length and rarely along the shoreline. Little structure was available in the canal and it appeared that the shoreline provided the only cover for largemouth bass. Though most of the study canal was 0.5 m deep, a 1.5 m deep trench existed along the southern shoreline, which may be the reason largemouth bass concentrated their daily movements along this shoreline. Interestingly, marsh largemouth bass may move further away from the shoreline at night when large predators are less abundant. High summer salinites can exceed levels preferred by largemouth bass, but predation risk may override the tendency of small marsh bass to seek less saline waters. Therefore, predation risk may influence both daily and seasonal movements of largemouth bass in coastal areas.

CHAPTER 5. BEHAVIOR OF LARGEMOUTH BASS IN RESPONSE TO A SALINITY GRADIENT

ABSTRACT

Salinity preferences of adult and young-of-the-year (YOY) largemouth bass from a freshwater lake and brackish marsh were tested at 22°C in salinity gradient chambers (0, 3, 6, 9, 12 ppt) during a 12L:12D photoperiod. YOY largemouth bass from both collection sites preferred 0 ppt. Although adult marsh and freshwater largemouth bass preferred 3 ppt, differences in salinity selection were noted; mean number of observations at 0 ppt was significantly greater for freshwater bass while mean number of observations at 3 ppt was significantly greater for marsh bass. Salinity preferences were not affected by a two-week acclimation to salinities of 0 or 5 ppt. Differences in salinity selection of adult largemouth bass between collection sites may be the result of long-term exposure to salinity.

INTRODUCTION

Swingle and Bland (1974) suggested that marsh bass make seasonal movements through waters of varying salinities. For fishes that migrate between freshwater and brackish habitats, salinity preferences directly influence movements (Houston 1957, Holliday 1971, Audet et al. 1985). Baggerman (1957) showed that salinity preferences in fish populations can also vary among age groups and with acclimation. In this study, I used salinity preference experiments to evaluate behavioral responses of adult and young-of-the-year (YOY) largemouth bass from a freshwater lake and brackish marsh to salinity gradients in the laboratory. The influence of acclimation to salinity on preferences was also examined.

METHODS

During the spring of 1986, adult (190-250 mm total length) and YOY (65-90 mm total length) largemouth bass were collected from the marsh and from Ben Hur Lake. All fish were transported to the laboratory where they were held in 38-L tanks (one adult or six YOY per tank). Marsh bass were held in a 5 ppt artificial sea-water solution (Instant Ocean) and freshwater bass at 0 ppt. All were allowed one week to recover from capture stress and fed live golden shiners (Notimegonus crysoleucas) at a rate of about 2% body weight per day. Water temperature was maintained at 22°C under a 12L:12D photoperiod.

The effects of collection site, acclimation, and life stage on salinity preferences of largemouth bass were evaluated using four groups of 12 fish each: marsh bass adults, marsh bass YOY, freshwater bass adults, and freshwater bass YOY. Six fish from each marsh bass group were acclimated to 0 ppt salinity (decreased 1 ppt per day for 5 days), while six fish from each freshwater bass group were acclimated to 5 ppt salinity (increased 1 ppt per day for 5 days).

A salinity gradient device (Staaland 1969, Fivizzani and Spieler 1978) that consisted of five compartments (0.25 m^2 each) containing water of 0, 3, 6, 9, and 12 ppt salinity respectively (Figure 5.1). Though the water was not aerated, after each experiment the tank was drained, refilled, and the gradient reestablished. Dissolved oxygen concentrations were monitored before and after each test using a YSI Model 51B oxygen meter and always exceeded 7.0 ppm. Salinities were monitored (YSI Model 33 salinometer) before and after each test. Water temperature in the tank was maintained at 22°C.

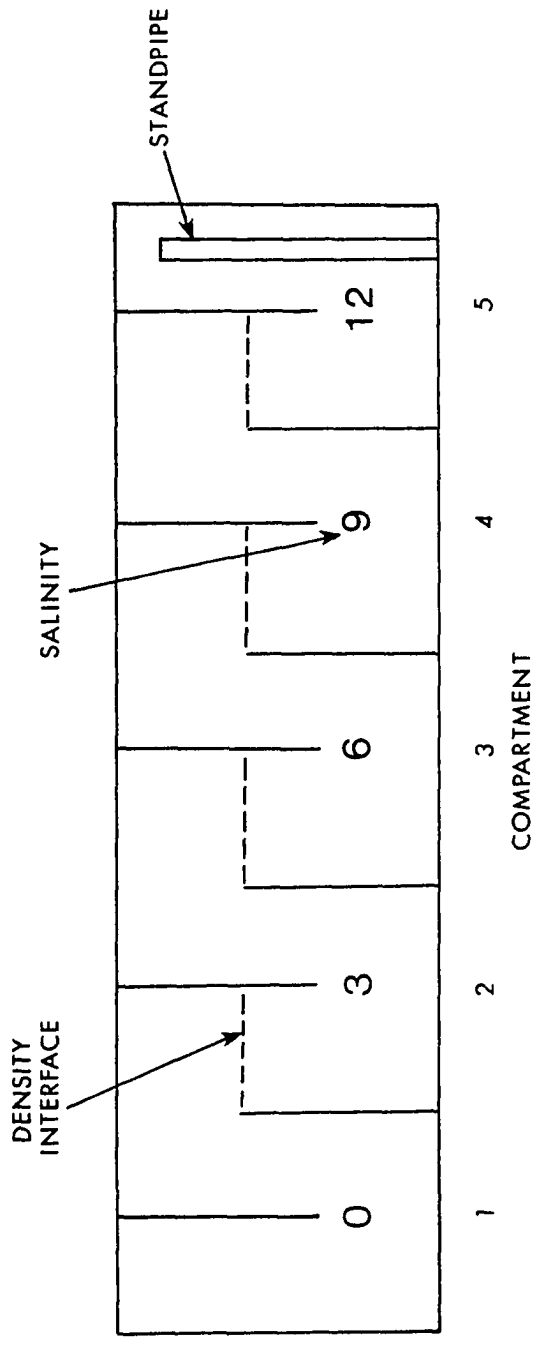

Figure 5.1. Lateral view of the salinity gradient device.

Individual fish were placed into the freshwater compartment (0 ppt) and allowed to habituate for one hour before testing. Preliminary trials indicated at least one hour was necessary for fish to explore the tank. Positions of individual fish in the tank were observed every 30 minutes for a total of 18 observations per individual. Salinity preference, based on the mean number of observations in each compartment, and the mean of salinities selected were determined for each experimental group. Twelve adult freshwater largemouth bass were tested individually in the tank without a salinity gradient (0 ppt in each compartment) as experimental controls. Of these fish, six were introduced into one end compartment and six into the opposite end compartment. During all experiments, each fish was used only once.

All data were analyzed using SAS (SAS Institute Inc. 1985). Chi-square analysis were used to evaluate control preferences. A repeated measures analysis of variance was used to test differences in salinity preference. Statistical significance was declared at the $P<0.05$ level.

RESULTS

No differences were detected between observed and expected frequency distributions of preference observations without a salinity gradient. Fish spent approximately equal time in all compartments and the compartment into which the fish were introduced did not influence position in the tank (Figure 5.2). Therefore, subsequent preferences were assumed to be influenced only by salinity in the present study.

YOY largemouth bass from both collection sites preferred 0 ppt salinity (Figure 5.3). No differences in salinity preference were observed between YOY marsh and freshwater bass and acclimation did not influence salinity preference. The mean of salinities selected by YOY bass from each site, acclimated to 0 ppt, was 1.8 ppt. The mean of salinities selected by YOY bass acclimated to 5 ppt was 1.4 ppt for marsh bass and 1.5 ppt for freshwater fish.

Adult largemouth bass from both collection sites preferred 3 ppt salinity. However, mean number of observations at 0 ppt was greater for freshwater largemouth bass (Figure 5.4). In contrast, mean number of observations at 3 ppt was significantly greater for marsh bass. No other differences in mean number of observations were detected between adult marsh and freshwater largemouth bass. Acclimation to 0 or 5 ppt salinity did not influence adult largemouth bass salinity preferences. The mean of salinities selected by adult bass acclimated to 0 ppt was 4.1 ppt for marsh bass and 3.5 ppt for freshwater fish. The mean of salinities selected by adult bass acclimated to 5 ppt was 3.8 ppt and 3.1 ppt for marsh and freshwater bass respectively.

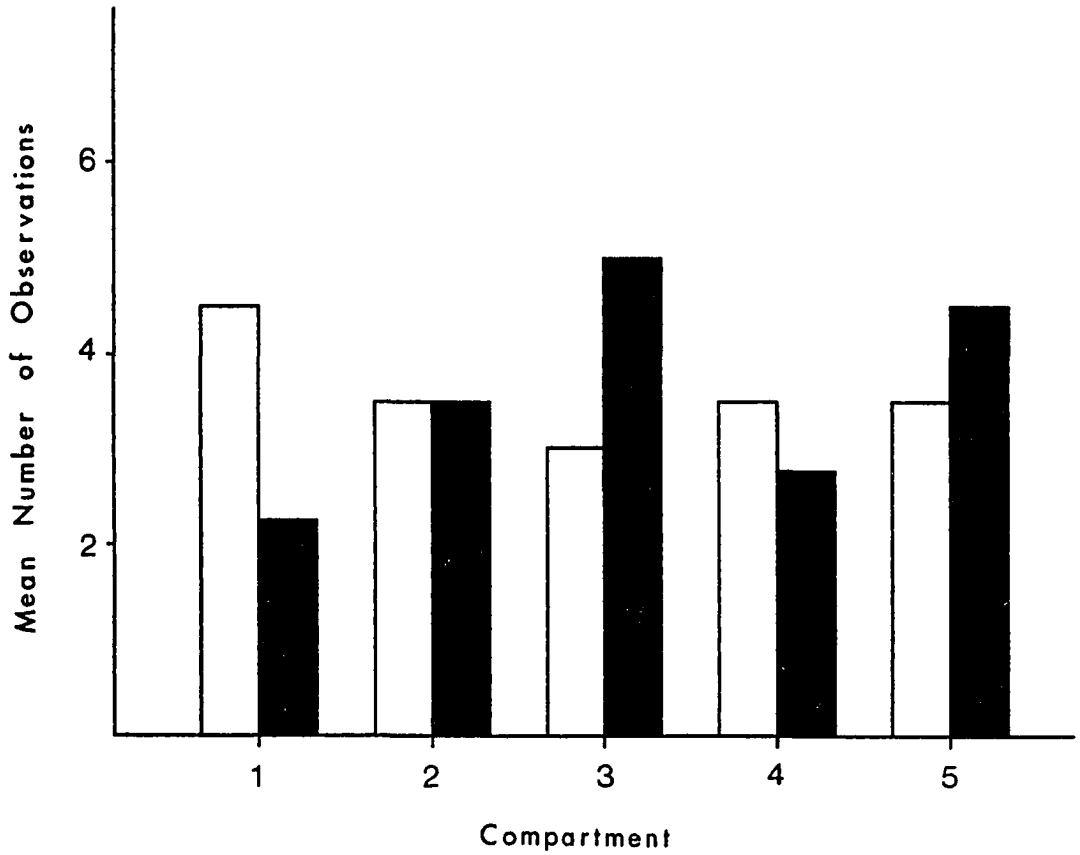

Figure 5.2. Mean number of observations of largemouth bass in each compartment under control conditions (0 ppt salinity in all compartments). Solid bars represent fish introduced into compartment 5 (6 fish, 18 observations/fish); open bars represent fish introduced into compartment 1 (6 fish, 18 observations/fish).

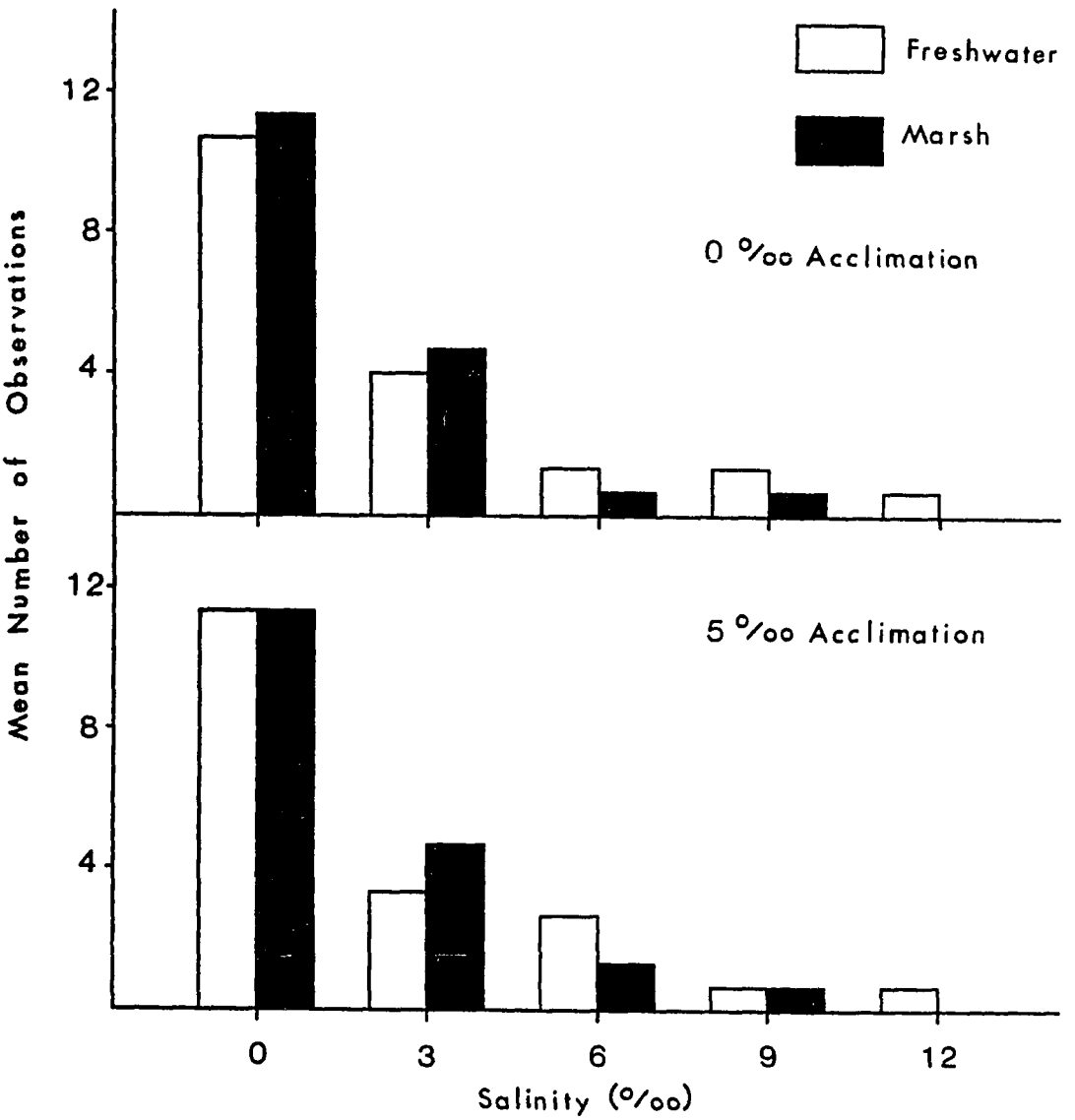

Figure 5.3. Mean number (6 fish per site, 18 observations/fish) of salinity selection observations of young-of-the-year freshwater and marsh largemouth bass acclimated to 0 (top) and 5 (bottom) ppt salinity.

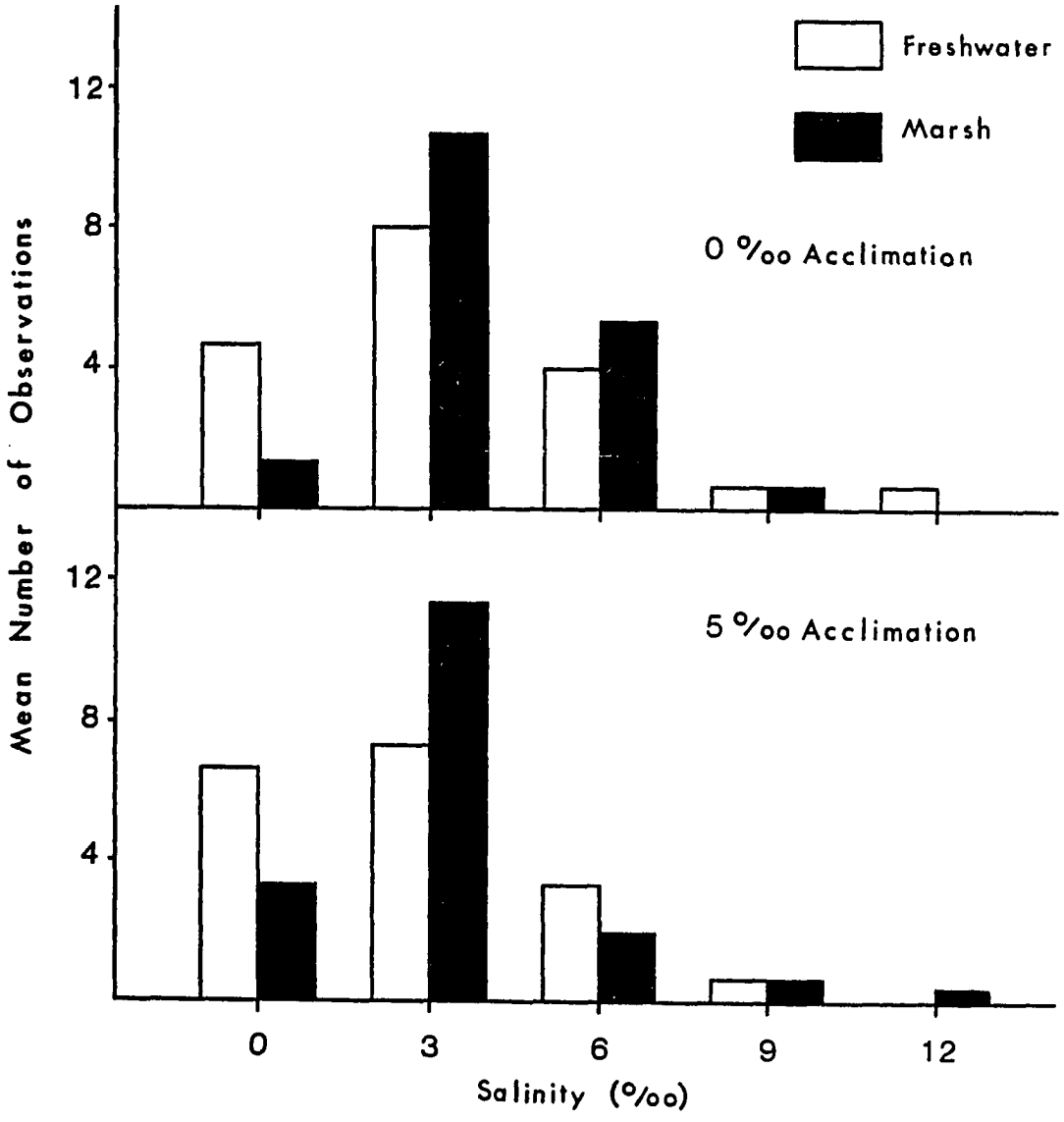

Figure 5.4. Mean number (6 fish per site, 18 observations/fish) of salinity selection observations of adult freshwater and marsh largemouth bass acclimated to 0 (top) and 5 (bottom) ppt salinity.

Acclimation data were combined to test salinity preferences between adult and YOY largemouth bass for each collection site. While mean number of observations at 0 ppt was greater for YOY largemouth bass, mean number of observations at 3 and 6 ppt were greater for adult fish (Figure 5.5). No differences were detected at 9 or 12 ppt between adult and YOY fish. The mean of salinities selected by adults was 3.6 ppt for marsh bass and 3.1 ppt for freshwater bass. The mean of salinities selected by YOY fish was 1.7 ppt for freshwater bass and 1.6 ppt for marsh bass.

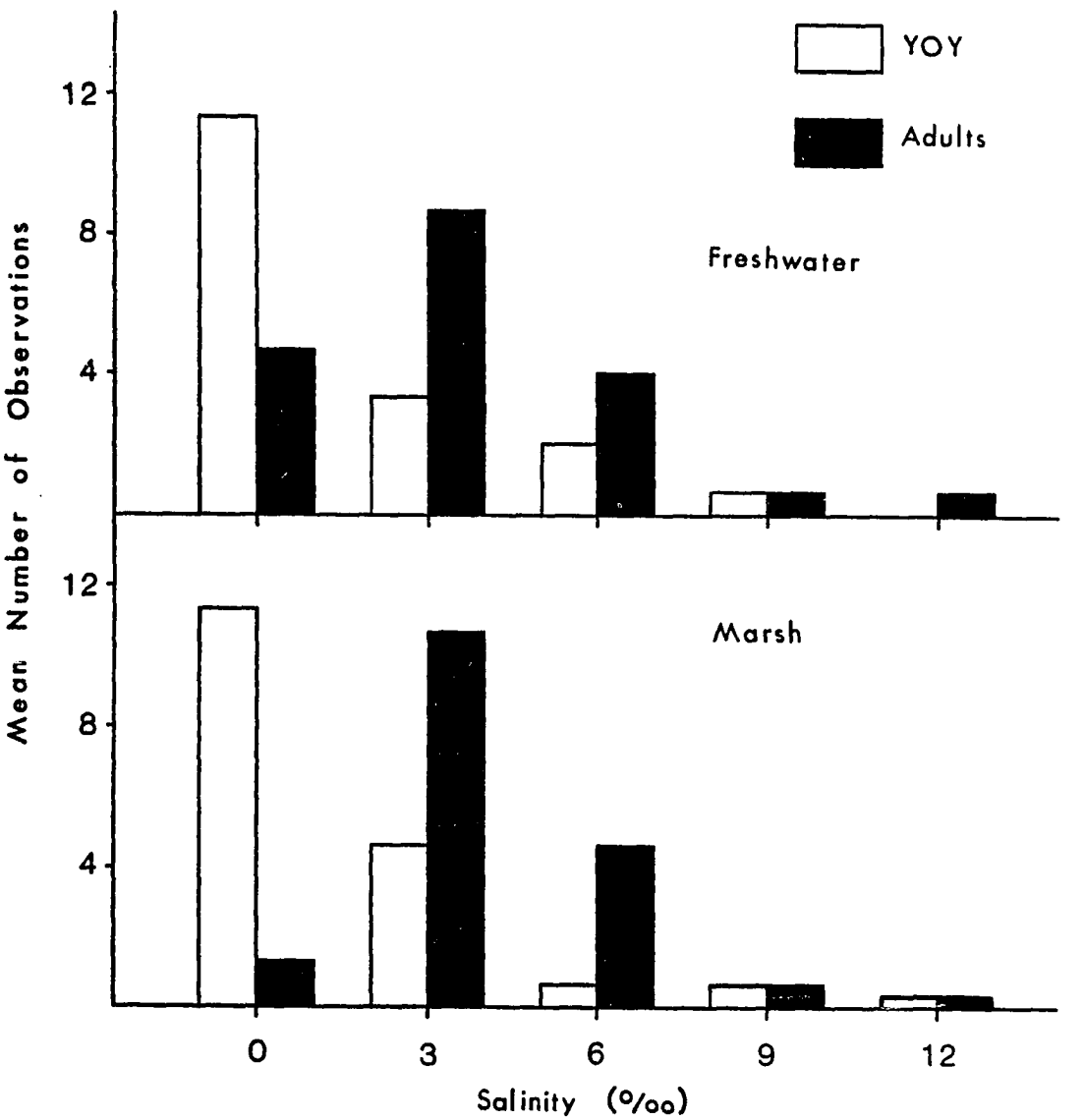

Figure 5.5. Mean number (12 fish per site, 18 observations/fish) of salinity selection observations of young-of-the-year (YOY) and adult largemouth bass from freshwater (top) and brackish marsh (bottom).

DISCUSSION

Adult and YOY largemouth bass from both collection sites preferred salinities of 4 ppt or less. The ability to select a salinity along a salinity gradient is critical to reproductive success (Fitzgerald and Wootton 1986). Neely (1962) reported that largemouth bass reproduction ceases at salinities greater than 3 ppt. Bulkley (1975) stated that largemouth bass should not be expected to maintain normal populations in waters in which they are continously exposed to more than 3.5 ppt salinity. Salinity preferences of largemouth bass in the present study were similar to these 'critical' salinity values of 3.0 and 3.5 ppt.

Interestingly, biotelemetry studies indicated that adult marsh bass avoided salinities above 5 ppt. However, even when salinities exceeded 8 ppt, small (<270 mm) marsh bass were still present in the study area. Biotlemetry data contrast with salinity preference results, which indicated a lower salinity preference for smaller marsh bass. Although the presence of smaller bass in marshes at elevated salinities has been reported previously (Swingle and Bland 1974), how and why they remain in such habitats is unknown. One possibility is that risk of predation from large marsh predators such as alligators (Alligator mississippiensis) and alligator gar (Lepisosteus spatula) restricts movements of smaller individuals, similar to interactions among other freshwater centrarchids (Mittlebach 1981, 1984).

Salinity preferences of largemouth bass were not affected by salinity acclimation. Fritz and Garside (1974) reported that the absence of an acclimation effect on salinity preference of mummichogs (Fundulus heteroclitus) indicated that these fish possessed the ability to adapt

rapidly to changes in salinity. Marsh bass appear to possess a similar ability within the range of acclimation levels tested in this study. Such an ability would be necessary to sucessfully inhabit coastal marshes in Louisiana, as salinity fluctuations of 1-3 ppt over a few days were common in the study area throughout the summer and fall depending on wind patterns and rainfall.

Differences in salinity selection between adult marsh and freshwater largemouth bass corresponded to natural habitat salinities. However, no differences were detected in YOY salinity between collection sites. Similarity in YOY salinity preference between marsh and freshwater largemouth bass was most likely related to low (near 0 ppt) spring salinities in the marsh resulting from substantial freshwater input. Salinities increased during summer and fall, thus differences in salinity preference between adult marsh and freshwater largemouth bass and the lack of similar variation between YOY fish was probably the result of acclimitization to salinity.

Ontogenetic changes in salinity preferences of fishes have been reported previously (Otto and McInerney 1970, Reynolds and Thomson 1974), and other studies suggest one preference may be related to habitat selection and another, nearer the blood isosmotic point, to a "physiological optimum" of minimum osmotic work (Houston 1957, Reynolds and Thomson 1974). In marsh bass, ontogenetic changes in salinity preferences appear to reflect prevailing marsh conditions, related primarily to seasonal influxes of fresh and salt water.

In addition to seasonal influxes of fresh and salt water, coastal marshes are frequently characterized in summer by high temperatures and low dissolved oxygen concentrations (>32^{o}C and <3 ppm respectively in the present study). The movement of many estuarine fishes into less saline waters during summer has been attributed to increasing temperature (Gunter 1967). Therefore, fluctuating salinity is only one of several environmental factors that influence habitat selection by marsh bass. While marsh bass must contend with a complex marsh physicochemistry, elevated salinity does appear to be of primary importance in determining seasonal abundance and movement patterns. It should be noted that many factors, such as water temperature, photoperiod, and thyroid activity are known to influence behavioral responses of fishes to salinity (Spieler et al. 1976, Miller et al. 1983, Audet et al. 1986), and it is likely that the influence of salinity on marsh bass ecology is a temporally and spatially complex phenomenon.

CHAPTER 6. PHYSIOLOGICAL CHARACTERISTICS OF LARGEMOUTH BASS EXPOSED TO SALINITY

ABSTRACT

Plasma osmotic and electrolyte concentrations as well as branchial Na^+/K^+ and Mg^{++} ATPase activities were determined in the field for largemouth bass from a brackish marsh and freshwater lake. Laboratory experiments were conducted to evaluate plasma chemistry and gill ATPase activities of largemouth bass from both collection sites exposed to 4, 8, and 12 ppt salinity. No significant differences in physiological characteristics were detected between marsh and freshwater largemouth bass exposed to 4 or 12 ppt. Exposure to 12 ppt salinity resulted in osmotic stress in largemouth bass from both collection sites. At 8 ppt, marsh bass had significantly higher plasma solutes and lower gill ATPase activities than freshwater fish. Differential physiological responses between marsh and freshwater largemouth bass suggest freshwater fish expend greater energy to maintain osmotic balance. Marsh largemouth bass appear to have adapted to environments of variable salinity by reducing energetic expenditures related to osmoregulation.

INTRODUCTION

Freshwater fishes that inhabit brackish environments must tolerate sometimes sudden and drastic fluctuations in salinity. Their ability to inhabit environments of variable salinity is dependent on ionoregulatory mechanisms that maintain proper osmotic balance. Gill ATPase activities, including the oubain-sensitive Na^{+}/K^{+} ATPase and the oubain-insensitive Mg^{++} ATPase, have been shown to play an important role in ionregulation and saltwater adaptation of freshwater euryhaline fishes (Epstein et al. 1967, Kamiya and Utida 1969, Towle et al. 1977). Failure of freshwater fishes to adapt to increased salinity results in increased electrolyte concentrations and osmotic stress (Davis and Simco 1976). The objective of this study was to examine the effects of salinity on plasma chemistry and gill ATPase activities of largemouth bass from a brackish marsh and freshwater lake. Plasma osmolality and electrolyte concentrations were used as indicators of osmoregulatory dysfunction.

METHODS

Field.-During fall 1987, adult (215-361 mm total length) largemouth bass were collected from the marsh and False River by electroshocking. Twelve fish from each location were sampled in the field within 10 minutes of initial disturbance. Each fish was anesthetized with MS-222 and blood was collected in lithium-heparinized Vacutainer tubes (Becton Dickinson, Vacutainer Systems, Rutherford, N.J.) from vessels in the caudal peduncle. Blood was transferred to 1.5 ml centrifuge tubes, centrifuged for 2 minutes at 13,750 rpm, and plasma removed with a disposable pipette. Plasma osmolality values were determined immediately after centrifugation using a 50-ul sample in a freezing-point depression osmometer (Precision Systems, Model 5004). A portable generator was used to provide electrical power. Remaining plasma was placed on dry ice and transported to the laboratory where it was stored at -77°C for analysis of ion content. Gill filament was trimmed from gill arches, placed on dry ice, transported to the laboratory, and stored at -77°C for analysis of gill Na^+/K^+ ATPase and Mg^{++} ATPase activity. Sodium, potassium, magnesium, and calcium levels were determined simultaneously using inductively coupled plasma (gas) atomization (Applied Research Laboratories, Model 34000). Chloride concentrations were determined with a Haake Buchler digital chloridometer (Model 4425). Branchial ATPase activities were determined by the method of Zaugg (1982). Protein concentrations in the enzyme preparations were determined using the Bio-Rad protein assay (Bio-Rad Laboratories, Richmond, California).

Laboratory.-Largemouth bass from each location were transported to the laboratory and held in aerated fiberglass tanks containing 305 L of biofiltered tapwater at 0 ppt. Nitrite and ammonia levels were monitored

periodically and did not exceed 0.1 mg/l. All fish were allowed two weeks to recover from capture stress and fed live bluegill (Lepomis macrochirus) ad libitum daily. Water temperature was maintained at 22°C under a 14L:10D photoperiod. Twenty-four hours after the acclimation period, four largemouth bass per location were removed at 0 ppt and sampled for plasma chemistry and gill ATPase activities as previously described. Salinity was then increased 1 ppt per day using an artificial sea salt solution (Instant Ocean) and measured using a YSI Model 33 salinometer. At each of three experimental salinity levels (4, 8, and 12 ppt), four fish from each location were removed and sampled for plasma chemistry and gill ATPase activities at 6, 12, 24, 72, and 120 hours of exposure. Three fish from each location were sampled at 336 hours of exposure to 12 ppt.

All data were analyzed using the general linear model procedure of SAS (SAS Institute Inc. 1985). A two-way analysis of variance was used to evaluate plasma chemistry values between locations and with duration of exposure. Statistical significance was declared at the $P<0.05$ level.

RESULTS

Field Studies.-Although plasma calcium levels were greater for marsh bass than for freshwater bass, no other differences were detected in plasma chemistry values between marsh and freshwater fish (Table 6.1). The mean of each plasma variable $\pm$ 2 SD has been used to define 'normal' plasma values for largemouth bass (Carmichael et al. 1984). Therefore, data from both locations were combined to establish normal plasma osmotic and electrolyte values (Table 6.1). Plasma chemistry values observed during laboratory trials were compared to these normal ranges.

No differences in gill Na^+/K^+ ATPase or Mg^{++} ATPase activity were detected between marsh and freshwater largemouth bass. Mean gill Na^+/K^+ ATPase activity of marsh bass was 3.5 uMP_i mg $protein^{-1}$ hr^{-1} $\pm$ 1.3 SD with a range of 1.4-5.9. Gill Na^+/K^+ ATPase activities of freshwater largemouth bass ranged from 0.8-7.6 uMP_i mg $protein^{-1}$ hr^{-1} with a mean of 3.8 $\pm$ 1.8 SD. Mean gill Mg^{++} ATPase activity of marsh bass was 6.9 uMP_i mg $protein^{-1}$ hr^{-1} $\pm$ 2.4 SD with a range of 4.1-11.3. Gill Mg^{++} ATPase activity of freshwater largemouth bass ranged from 3.1-12.7 uMP_i mg $protein^{-1}$ hr^{-1} with a mean of 8.2 $\pm$ 3.5 SD.

Laboratory Studies.-No differences in plasma osmotic or electrolyte concentrations were detected between marsh and freshwater bass held at 0 ppt, and plasma chemistry values were within normal ranges (Table 6.2). No differences in plasma chemistry were detected at 4 ppt (see Appendix; Fig. A.1-A.6). At 8 ppt, plasma osmolality, sodium, chloride, and potassium levels were greater for marsh bass (Fig. A.7-A.10). However, magnesium and calcium levels were not different between plasma of marsh and freshwater fish (Fig. A.11, A.12). Plasma chloride and potassium

Table 6.1. Plasma osmotic and electrolyte concentrations (mean ± SD and range) of largemouth bass collected at 0 ppt salinity from a brackish marsh (N=12) and freshwater lake (N=12). Normal ranges were established from mean values ± 2 SD (locations combined). (Electrolytes are expressed in milliequivalents/liter, mOsm=milliosmoles).

	Osmolality (mOsm/L)	Na^+	Cl^-	K^+	Mg^{++}	Ca^{++}
Marsh	311±6.4 297-320	127.9±36.4 96.7-180.0	101.2±4.2 92.5-110.6	2.8±0.7 1.9-4.2	2.3±0.8 1.3-3.7	5.9±1.9 3.4-9.3
Freshwater	306±6.7 297-321	114.7±23.4 95.0-171.0	99.9±4.9 94.6-112.7	2.7±0.5 1.9-3.6	1.9±0.4 1.5-3.1	4.9±0.5 3.6-5.1
Normal Ranges	295-323	60-183	91-110	2-4	1-4	2-9

Table 6.2. Plasma osmotic and electrolyte concentrations (mean ± SD and range) of largemouth bass from a brackish marsh (N=4) and freshwater lake (N=4) held at 0 ppt salinity in the laboratory. (Electrolytes are expressed in milliequivalents/liter, mOsm=milliosmoles).

	Osmolality (mOsm/L)	Na^+	Cl^-	K^+	Mg^{++}	Ca^{++}
Marsh	311±7.9	127.9±15.3	94.0±4.1	2.3±0.6	2.0±0.2	5.8±1.3
	299-316	113.1-147.1	88.1-97.3	1.4-2.8	1.8-2.3	4.5-7.2
Freshwater	310±1.7	127.2±11.3	96.4±2.0	3.0±0.4	1.9±0.1	4.7±1.0
	308-312	112.8-138.9	94.3-99.1	2.6-3.5	1.7-2.0	3.6-6.0

concentrations varied with duration of exposure to 8 ppt, although no clear pattern was observed. No other differences in plasma chemistry were detected with duration of exposure to 8 ppt salinity. All mean plasma chemistry values were within normal ranges during exposure to 4 and 8 ppt.

Plasma osmotic and electrolyte concentrations increased with increased exposure to 12 ppt (Fig. A.13-A.18), but no differences in plasma chemistry were detected between marsh and freshwater largemouth bass at this salinity. Fish from both locations stopped feeding within 48 hours of exposure to 12 ppt and mean plasma chemistry values, with the exception of calcium, exceeded normal ranges during exposure to 12 ppt.

No differences in gill Na^+/K^+ ATPase or Mg^{++} ATPase activity were detected between marsh and freshwater largemouth bass held at 0 ppt. Mean gill Na^+/K^+ ATPase of marsh bass was 3.2 uMP_i mg $protein^{-1}$ hr^{-1} $\pm$ 2.4 SD with a range of 1.3-6.6. Gill Na^+/K^+ ATPase activities of freshwater largemouth bass at 0 ppt ranged from 1.9-4.9 uMP_i mg $protein^{-1}$ hr^{-1} with a mean of 3.2 $\pm$ 1.3 SD. Mean gill Mg^{++} ATPase activity of marsh bass at 0 ppt was 6.9 uMP_i mg $protein^{-1}$ hr^{-1} $\pm$ 2.4 SD with a range of 4.9-10.5. Gill Mg^{++} ATPase activity of freshwater largemouth bass at 0 ppt ranged from 3.9-7.6 uMP_i mg $protein^{-1}$ hr^{-1} with a mean of 5.8 $\pm$ 1.6 SD. No differences were detected in gill Na^+/K^+ ATPase or Mg^{++} ATPase activities at 4 or 12 ppt (Fig. A.19, A.20, and A.23, A.24). However, gill Na^+/K^+ and Mg^{++} ATPase activities were greater for freshwater largemouth bass at 8 ppt (Fig. A.21, A.22).

Duration of exposure data were combined to evaluate the influence of salinity on gill Na^+/K^+ and Mg^{++} ATPase activities of bass from each location. No differences in mean gill ATPase activities of marsh bass were detected among salinity levels. Mean gill ATPase activities of freshwater largemouth bass were not different among 0, 4, and 12 ppt. However, gill Na^+/K^+ and Mg^{++} ATPase activities of freshwater fish were greater at 8 ppt (Table 6.3).

Table 6.3. Mean gill Na^+/K^+ (NATP) and Mg^{++} (MATP) ATPase activities of largemouth bass from a brackish marsh and freshwater lake exposed to 0, 4, 8, and 12 ppt salinity. For each ATPase, means with the same letter are not significantly different (numbers in parenthesis indicate standard deviation).

	NATP		MATP	
Salinity	Marsh	Freshwater	Marsh	Freshwater
0	3.2 (2.4) A	3.2 (1.3) A	6.9 (2.5) A	5.8 (1.6) A
4	2.6 (1.3) A	3.3 (2.0) A	7.1 (2.4) A	7.3 (1.9) A
8	3.5 (1.9) A	6.0 (2.7) B	7.1 (2.0) A	13.3 (5.8) B
12	3.1 (1.9) A	3.9 (2.0) A	8.4 (2.6) A	9.1 (3.8) A

Discussion

Normal ranges of largemouth bass plasma values established from field data were similar to values previously reported for largemouth bass (Carmichael et al. 1984, Canfield et al. 1985, Williamson and Carmichael 1986). Although gill Na^+/K^+ and Mg^{++} ATPase activities have not been characterized for largemouth bass, Jampol and Epstein (1970) indicated that gill Na^+/K^+ ATPase activities of the congeneric smallmouth bass (Micropterus dolomieui) ranged from 1.0-6.0 uMP_i mg $protein^{-1}$ hr^{-1}, while Mg^{++} ATPase activities ranged from 11.5-15.4. Mg^{++} ATPase activities in the present study were generally lower than those reported for smallmouth bass. However, Na^+/K^+ ATPase activities in this study were in close agreement with those noted by Jampol and Epstein (1970). Therefore, laboratory observations were assumed to reflect the physiological characteristics of largemouth bass exposed to salinity.

Results of laboratory trials indicated that brief exposure of largemouth bass to 12 ppt can result in osmotic stress. While largemouth bass have been collected at salinities as high as 24 ppt (Bailey et al. 1954), Renfro (1959) indicated that salinities above 9 ppt were chronically lethal. Most freshwater teleost fishes maintain a blood osmolality of 265-325 mOsm (Bond 1979) indicating that they are isosmotic with 9-10 ppt salinity. Although largemouth bass are able to osmoregulate efficiently in hypotonic environments, exposure to a hypertonic medium can result in stress, with chronic exposure resulting in death.

The influence of salinities of 4 ppt or less on largemouth bass plasma values was minimal. Bulkley (1975) stated that largemouth bass

will not maintain normal populations in waters in which salinities are continually greater than 3.5 ppt, but implied that salinities less than 3.5 ppt had little effect on largemouth bass populations. To successfully inhabit coastal marshes of Louisiana, largemouth bass must be able to osmoregulate over a salinity range of 2-4 ppt for most of the year.

Differential physiological responses to 8 ppt were observed between marsh and freshwater largemouth bass, with marsh bass exhibiting significantly higher plasma chemistry values and lower gill ATPase activities than freshwater fish. Though no differences in plasma chemistry values (except calcium) or gill ATPase activities were detected between marsh and freshwater largemouth bass in the field at 0 ppt, marsh bass plasma solutes were generally higher while gill ATPase activites were lower. Greater gill ATPase activites and lower plasma chemistry values for freshwater largemouth bass suggest they expend greater energy to maintain osmotic balance than do marsh bass.

Hallerman et al. (1986) observed limited electrophoretic differences between marsh and freshwater largemouth bass and suggested that variation in growth rate and allometry between these populations was probably due to environmental factors. Coastal environments are typically shallow, resulting in summer water temperatures as high as 32^{o}C in Louisiana. Largemouth bass metabolic scope for activity, calculated by subtracting standard oxygen consumption from active, decreases at temperatures above 30^{o}C (Beamish 1970). To inhabit coastal environments, largemouth bass must endure seasonal osmotic and metabolic

demands. When faced with the increased energetic demands of seasonally fluctuating prey availability, largemouth bass have been reported to minimize standard and active metabolic demands (Adams et al. 1980). Therefore, marsh largemouth bass may have adapted to the seasonally fluctuating energetic costs of inhabiting coastal environments by reducing energetic expenditures.

CHAPTER 7. SUMMARY AND CONCLUSIONS

Largemouth bass from a Louisiana coastal marsh were small compared to similar age freshwater largemouth bass. Small size and slow growth rate of marsh bass relative to freshwater populations are characteristic of marsh bass throughout their range. Previous hypotheses generated to explain small size and slow growth rate of marsh bass have implied that marsh bass are stressed by physicochemical conditions inherent in brackish environments. Such potentially stressful conditions include high water temperature and low dissolved oxygen concentrations in summer as well as fluctuating salinity levels. However, such an assumption is not supported by marsh bass condition factors, which are typically high. In the present study, high relative weights throughout the year indicated an environment conducive to excellent growth. Therefore, marsh bass growth does not appear to be "poor", but merely different from that of their freshwater counterparts.

Though small size and slow growth are characteristic of marsh bass throughout their range, differences in length-at-age relative to freshwater populations were observed along the Atlantic and Gulf of Mexico coasts. Differences in food habits of marsh bass from Gulf and Atlantic coasts have also been reported. Marsh bass along the Atlantic coast appear to eat mostly fish, at proportions comparable to freshwater largemouth bass. Marsh bass from the Gulf coast consume a lower percentage of fish and a higher percentage of invertebrates. This may be due in part to the presence of large predators such as alligator gar (Lepisosteous spatula) that are common in Gulf coast brackish marshes.

In such habitats, predation risk may affect marsh bass habitat selection and foraging profitability, similar to interactions reported among other centrarchids.

Salinity was found to influence the growth of Louisiana largemouth bass. Laboratory trials consisting of 120-day exposure of marsh and freshwater largemouth bass to four salinity levels (0, 4, 8, and 12 ppt) indicated no significant differences ($P>0.05$) in specific growth rate of marsh bass held at 0, 4, and 8 ppt salinity. Similarly, no significant differences ($P>0.05$) were detected in specific growth rate of freshwater largemouth bass exposed to 0 and 4 ppt. However, growth of freshwater largemouth bass held at 8 ppt was significantly lower than growth at 0 ppt. All fish held at 12 ppt stopped feeding within weeks after the experiment began and died before the experiment ended.

The observed growth patterns of marsh bass appear to be a result of redistribution of somatic growth relative to freshwater fish, as evidenced by differences in body morphology between the two populations. Sheared principal components analysis of selected morphological measurements revealed that relative to freshwater fish, marsh bass were characterized by a deeper caudal peduncle, shorter fins, and a longer abdominal length. Although these measurements do not reveal specifically how growth characteristics of marsh and freshwater largemouth bass differ, they do indicate allometric differences between the two populations.

Ultrasonic telemetry of marsh bass suggested the existence of mobile and sedentary segments of marsh largemouth bass populations.

Though tagged fish could not be located after salinities reached 8 ppt, marsh bass smaller than tagged fish were collected in the study area. Salinity did not influence short term (daily) movements although salinity increases in late summer may have induced large-scale seasonal movements. Movements declined continuously from dawn to dusk and were significantly less at night.

Differences in behavioral responses to a salinity gradient were observed between marsh and freshwater largemouth bass. Salinity preference trials indicated that young-of-the-year (YOY) largemouth bass from a marsh and freshwater lake preferred 0 ppt salinity. No significant differences in salinity preference were observed between YOY marsh and freshwater bass and acclimation did not influence salinity preference. Adult largemouth bass from both collection sites preferred 3 ppt salinity. As with YOY bass, acclimation did not influence salinity preferences of adult largemouth bass. However, differences in salinity selection by adult bass between the two populations were noted and may be the result of long-term exposure to salinity.

If marsh bass growth patterns are a response to elevated or rapidly-fluctuating salinity, greater physiological efficiency of marsh bass could result in the observed trends in lengths-at-age. No significant differences in plasma osmotic and electrolyte concentrations or branchial Na^{+}/K^{+} and Mg^{++} ATPase activities were detected between marsh and freshwater largemouth bass exposed to 4 or 12 ppt salinity. Exposure to 12 ppt salinity resulted in osmotic stress in largemouth bass from both collection sites. However, at 8 ppt, marsh bass had

significantly higher plasma solutes and lower gill ATPase activities than freshwater bass, suggesting that freshwater fish expend greater energy to maintain osmotic balance.

In conclusion, marsh bass differ from their freshwater counterparts in size, growth rate, allometry, behavior, and physiology. On the basis of limited electrophoretic differences between marsh and freshwater largemouth bass, Hallerman et al. (1986) concluded that environmental factors were responsible for observed marsh bass growth patterns. It is unclear whether environmental factors alone are responsible for these observed differences. However, it is clear that salinity is not the only factor influencing marsh bass growth patterns. Marsh bass appear to have adapted to a complex interaction of physicochemical variables and biotic interactions inherent in low-salinity environments.

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APPENDIX

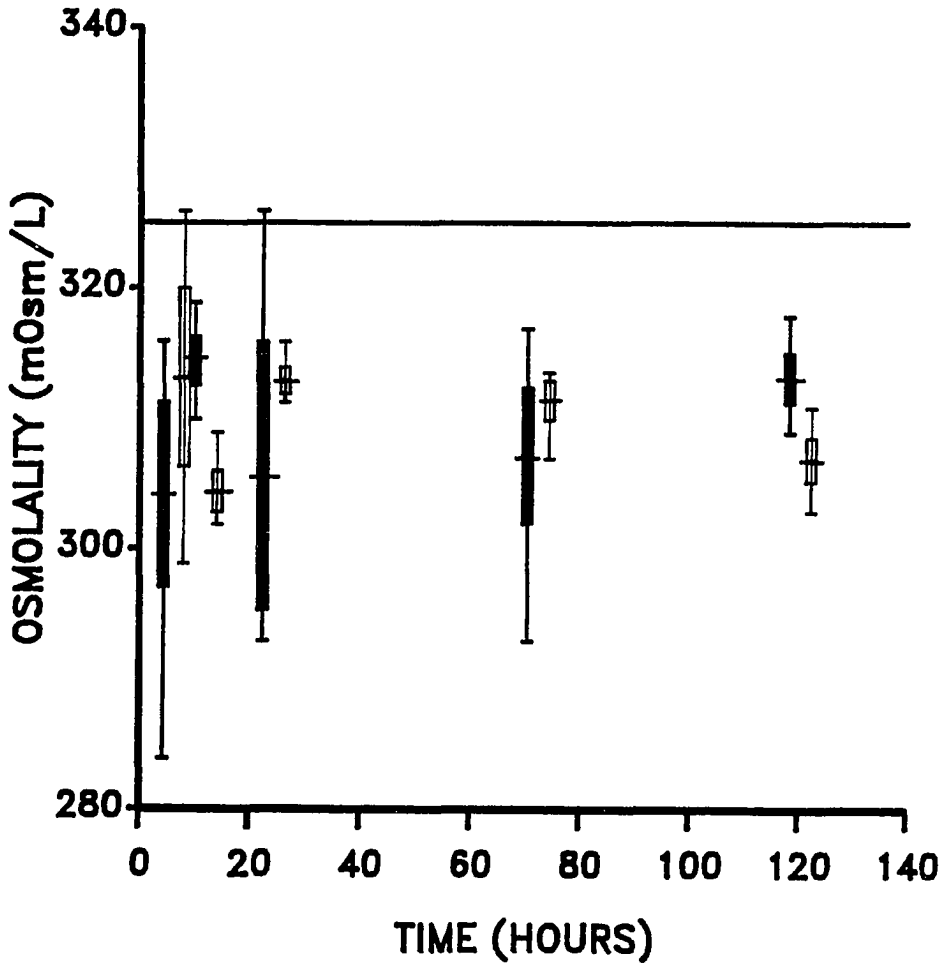

Figure A.1. Plasma osmolality (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 4 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma osmolality values.

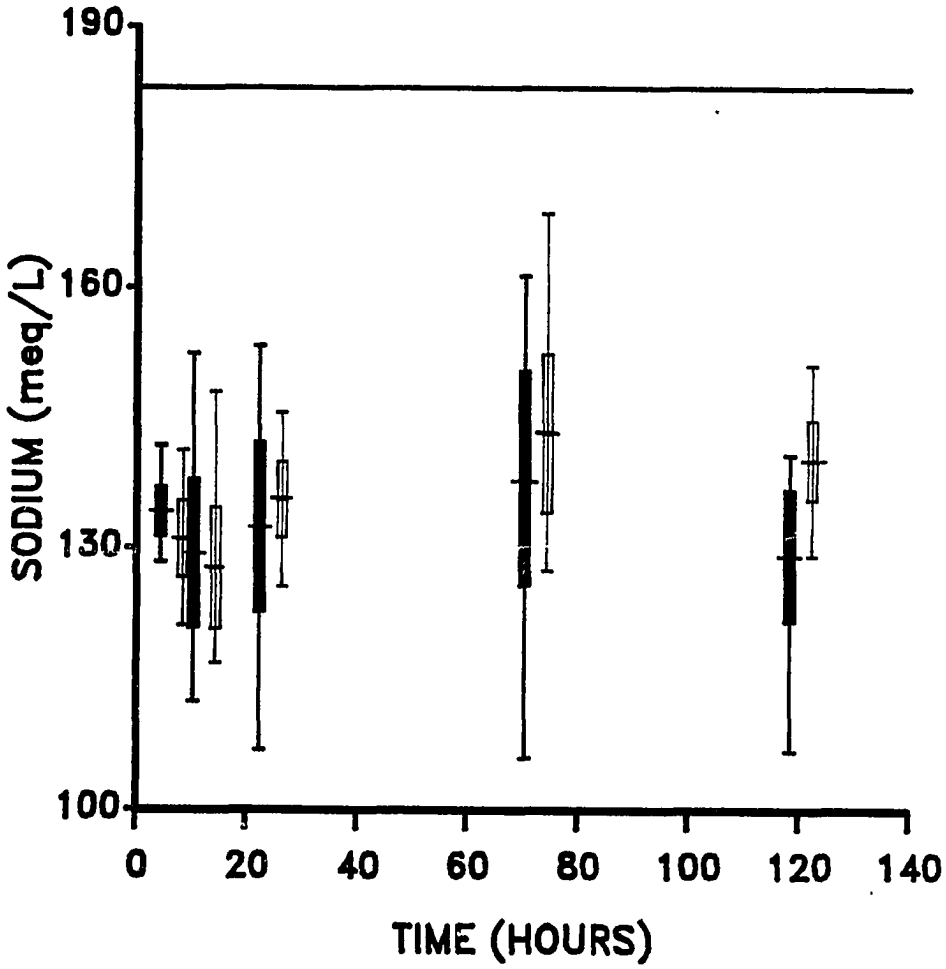

Figure A.2. Plasma sodium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 4 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma sodium values.

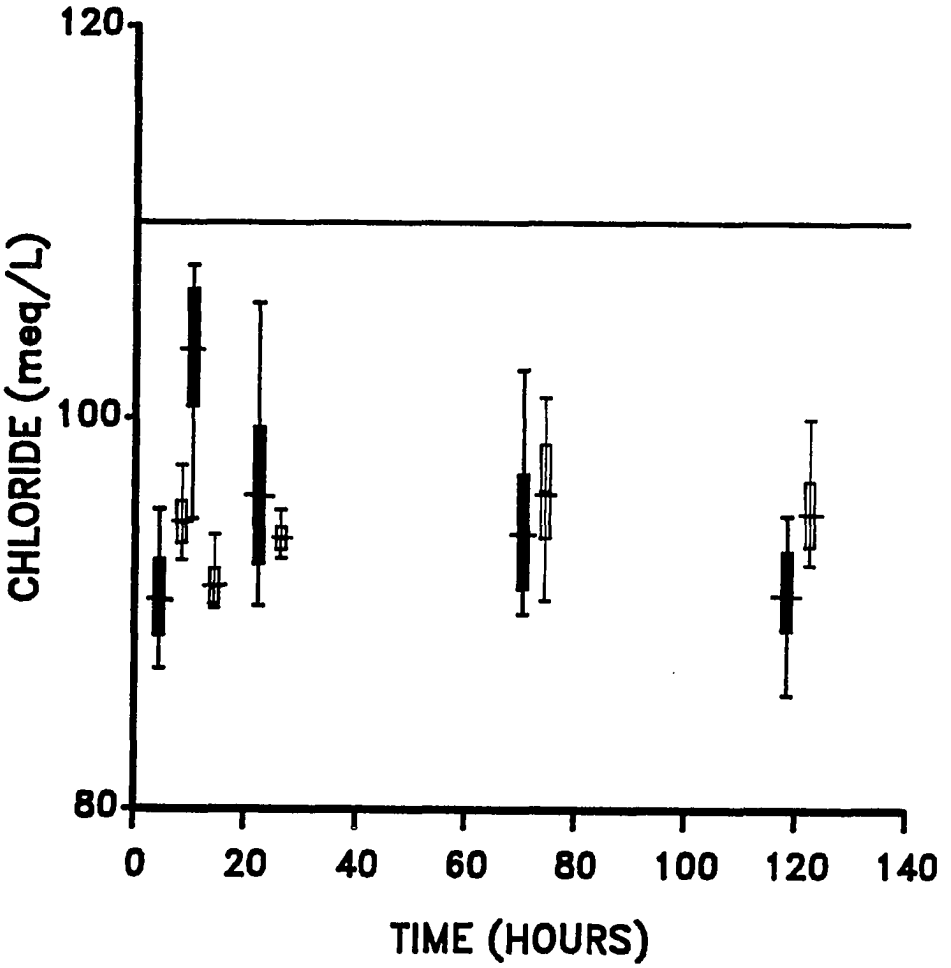

Figure A.3. Plasma chloride (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 4 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma chloride values.

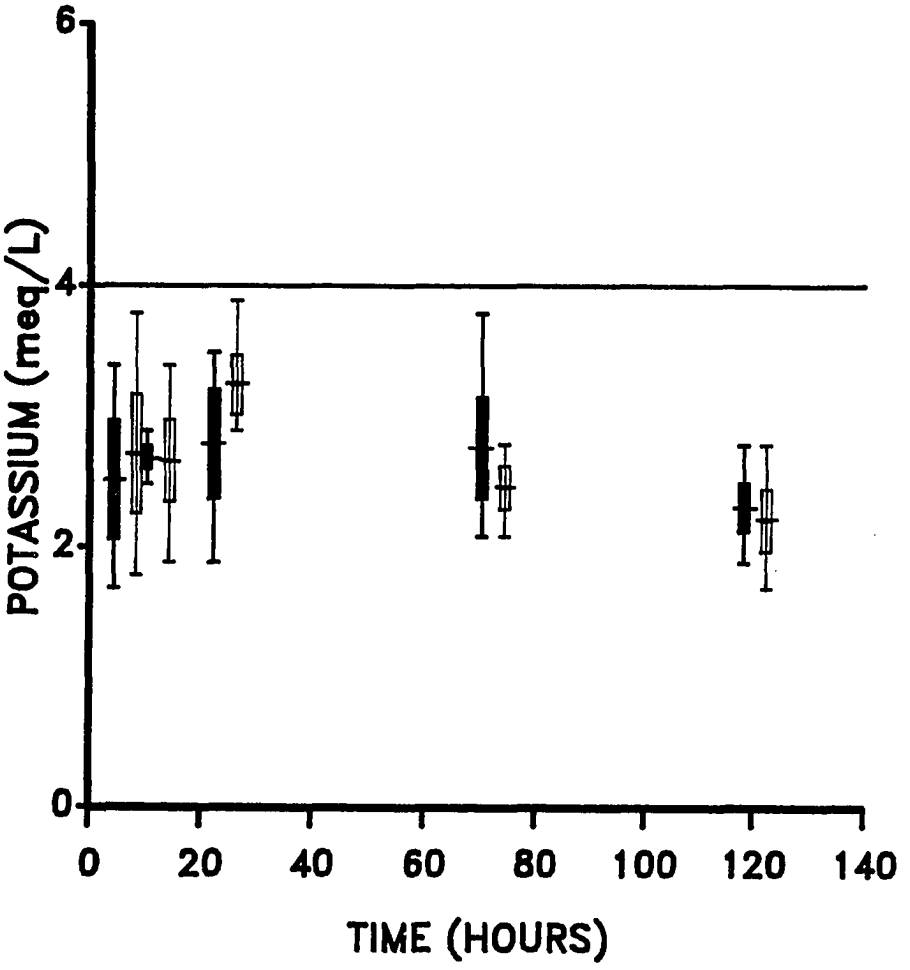

Figure A.4. Plasma potassium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 4 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma potassium values.

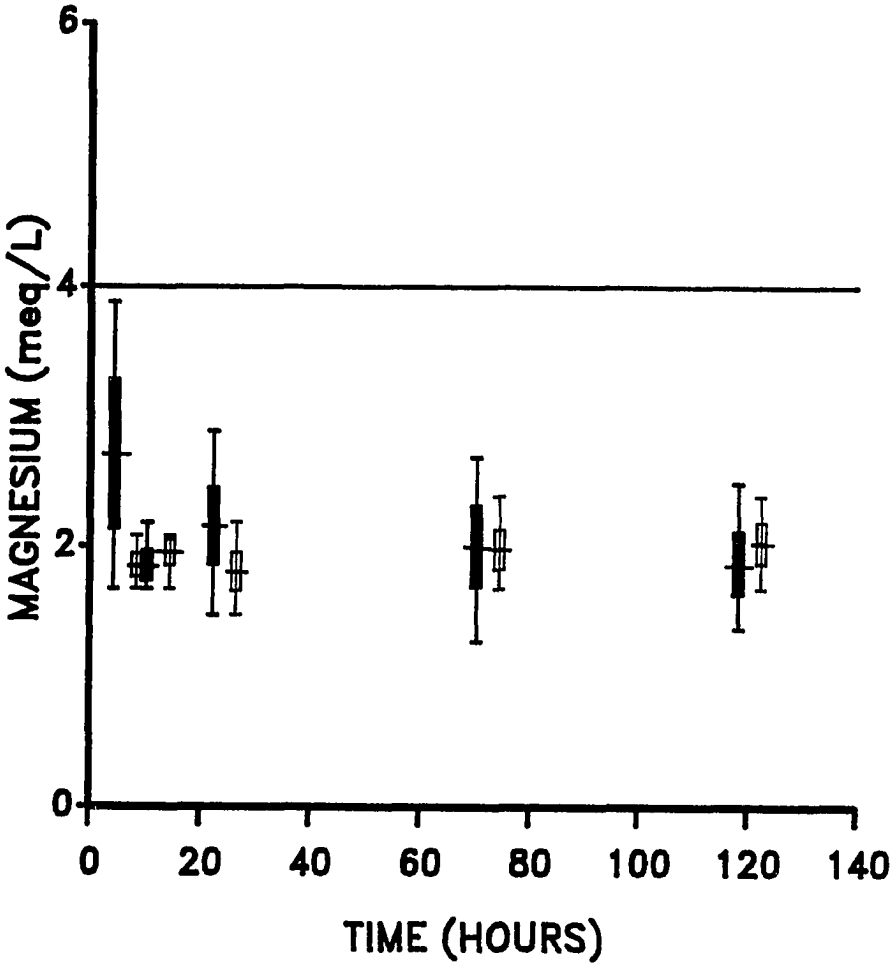

Figure A.5. Plasma magnesium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 4 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma magnesium values.

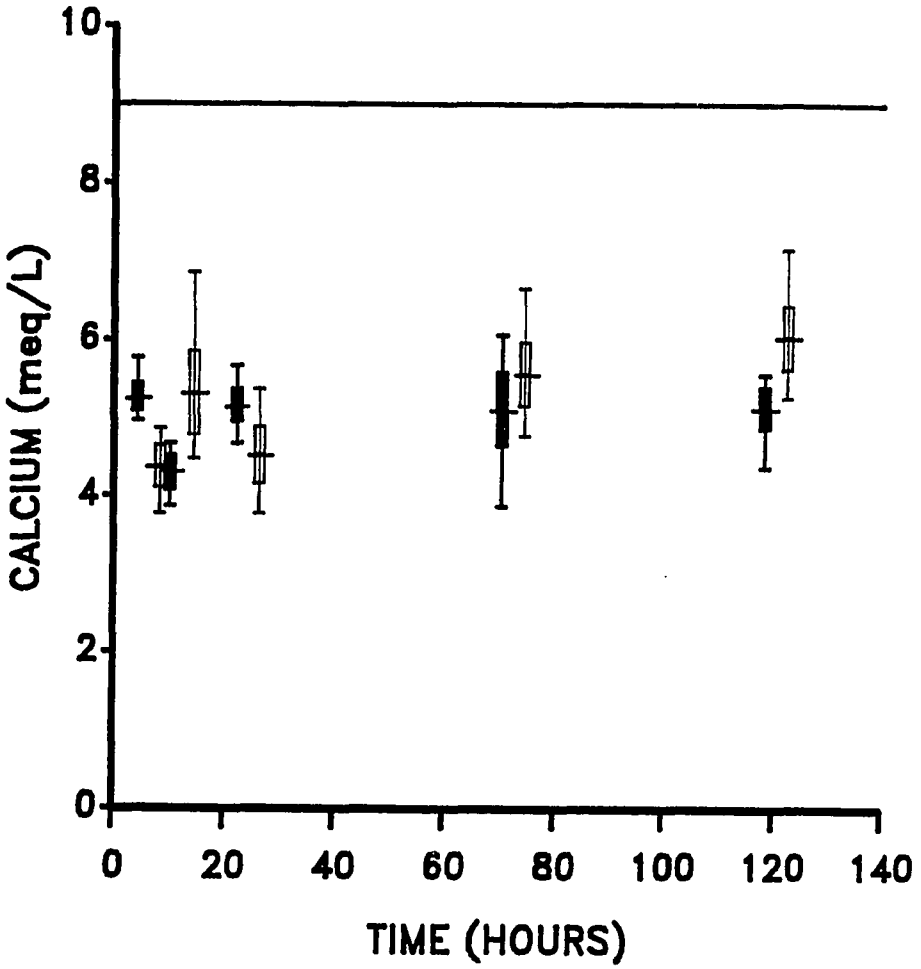

Figure A.6. Plasma calcium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 4 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma calcium values.

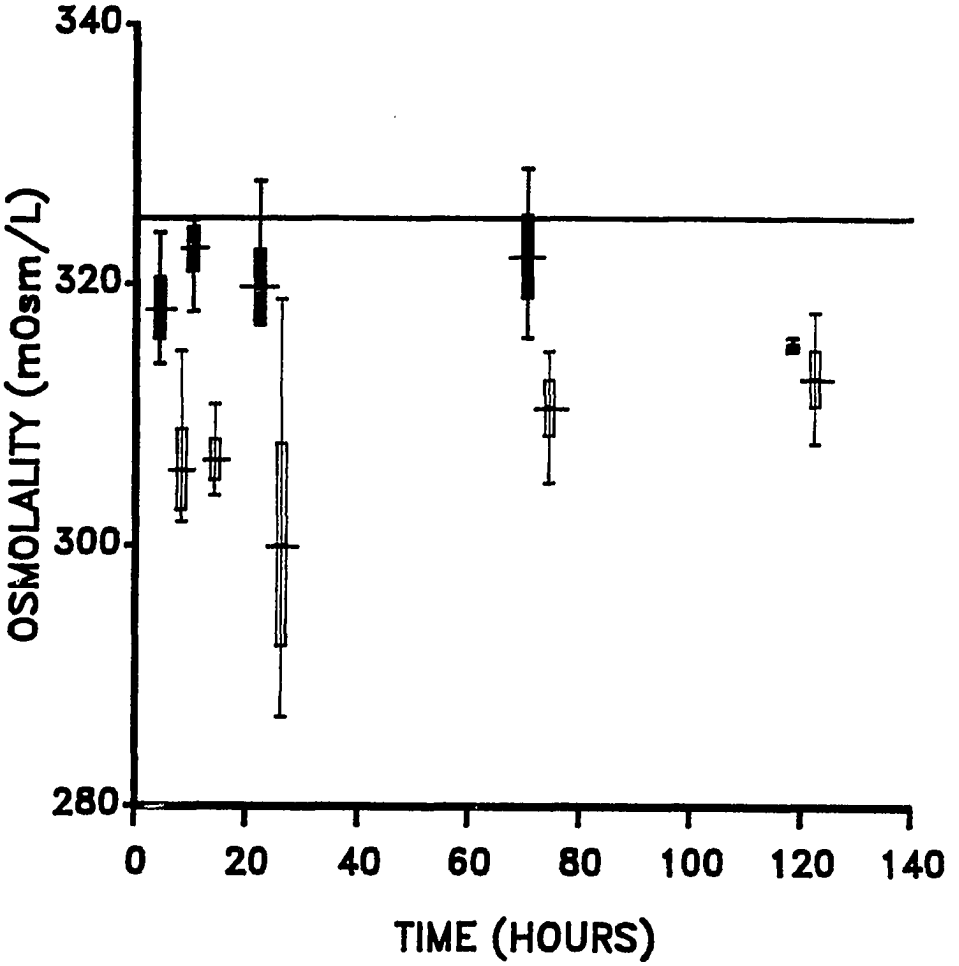

Figure A.7. Plasma osmolality (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 8 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma osmolality values.

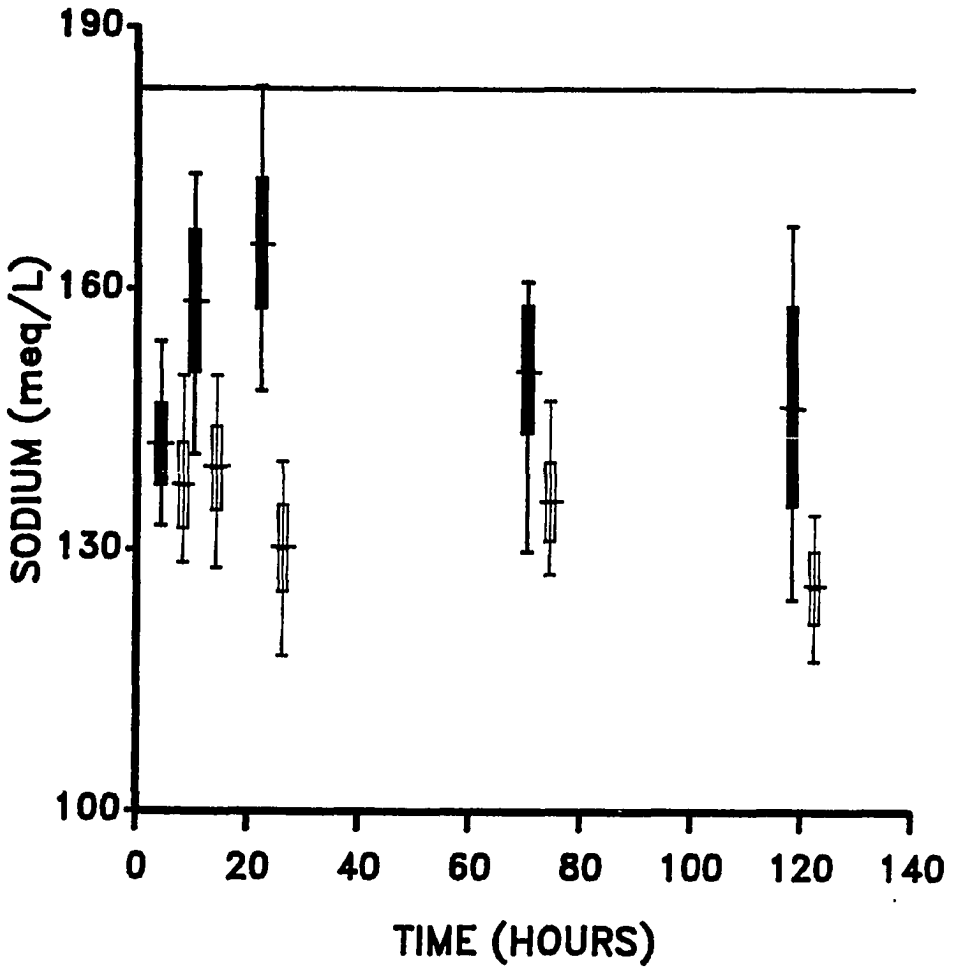

Figure A.8. Plasma sodium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 8 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma sodium values.

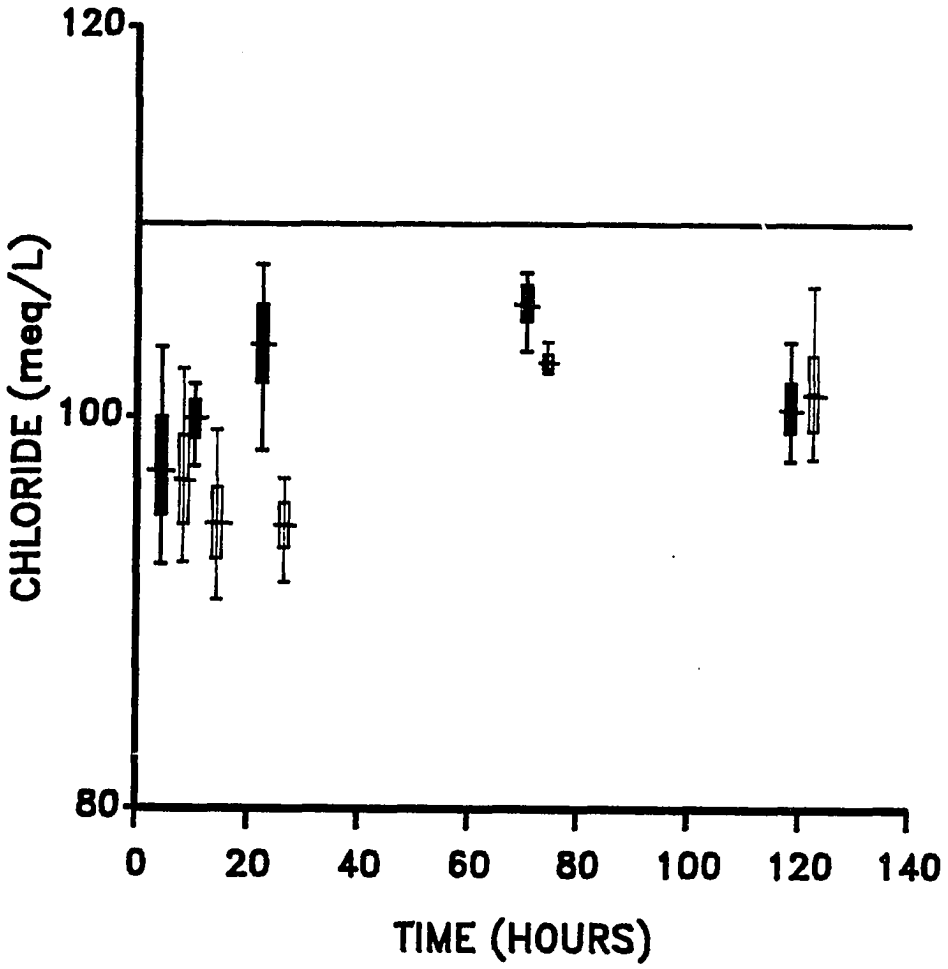

Figure A.9. Plasma chloride (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 8 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma chloride values.

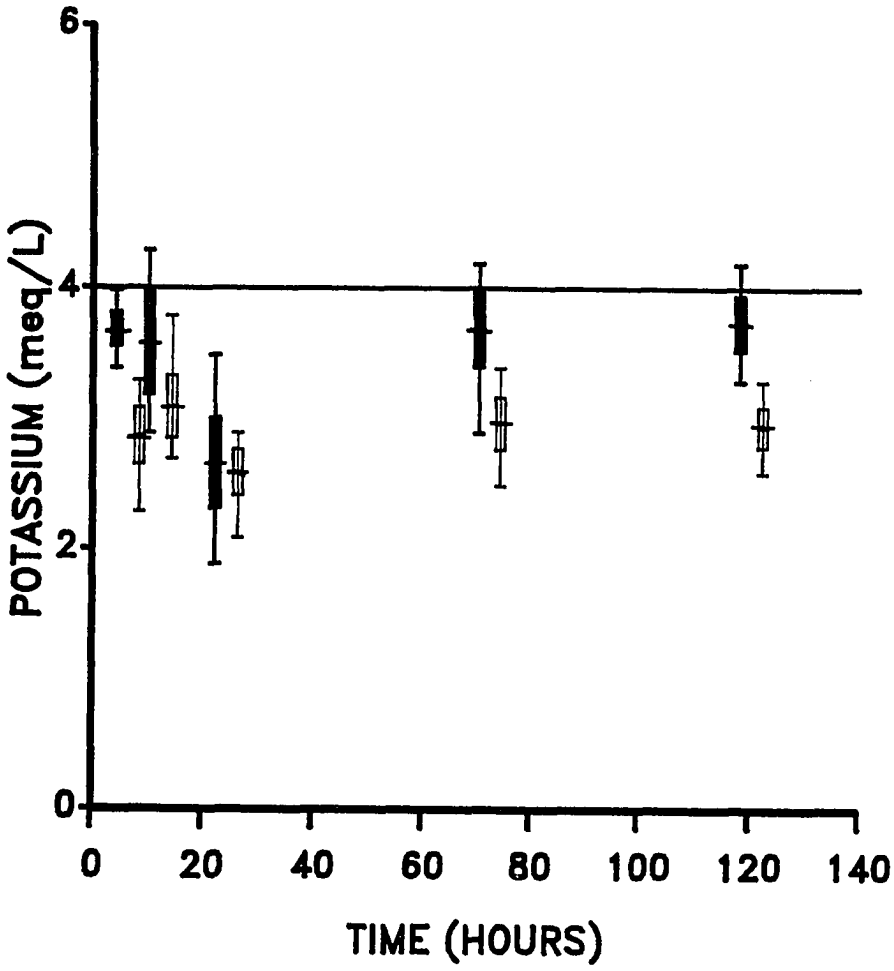

Figure A.10. Plasma potassium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 8 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma potassium values.

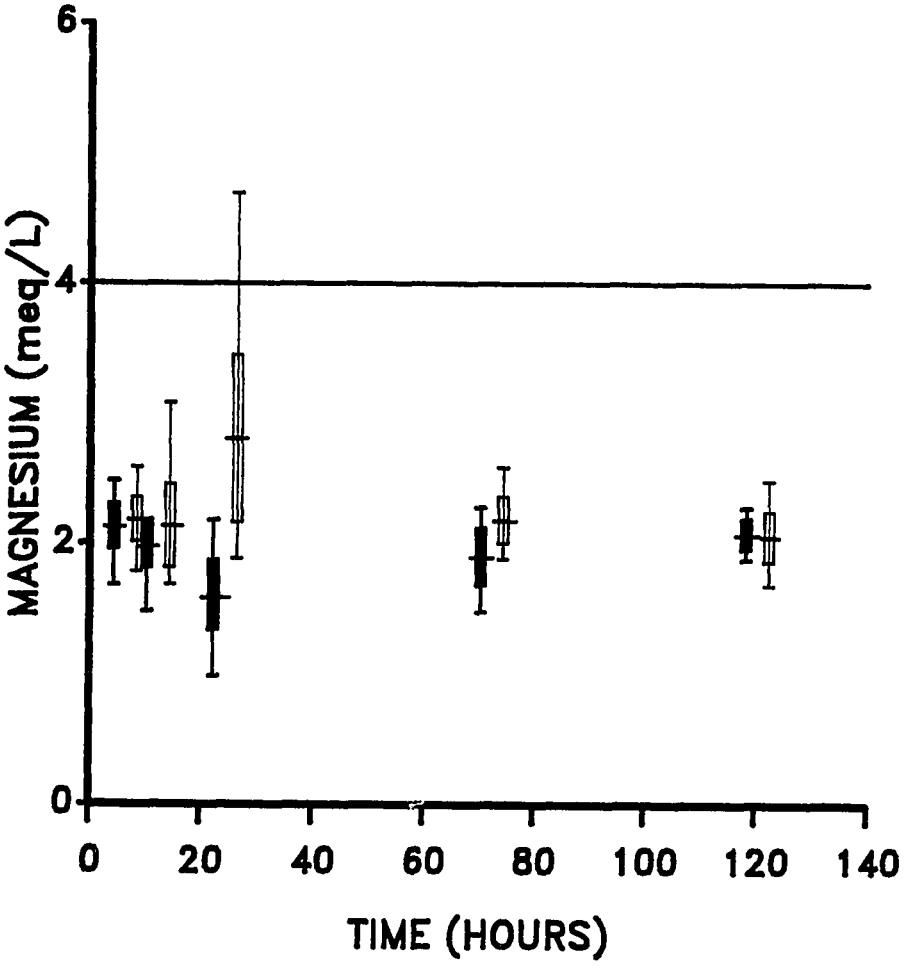

Figure A.11. Plasma magnesium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 8 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma magnesium values.

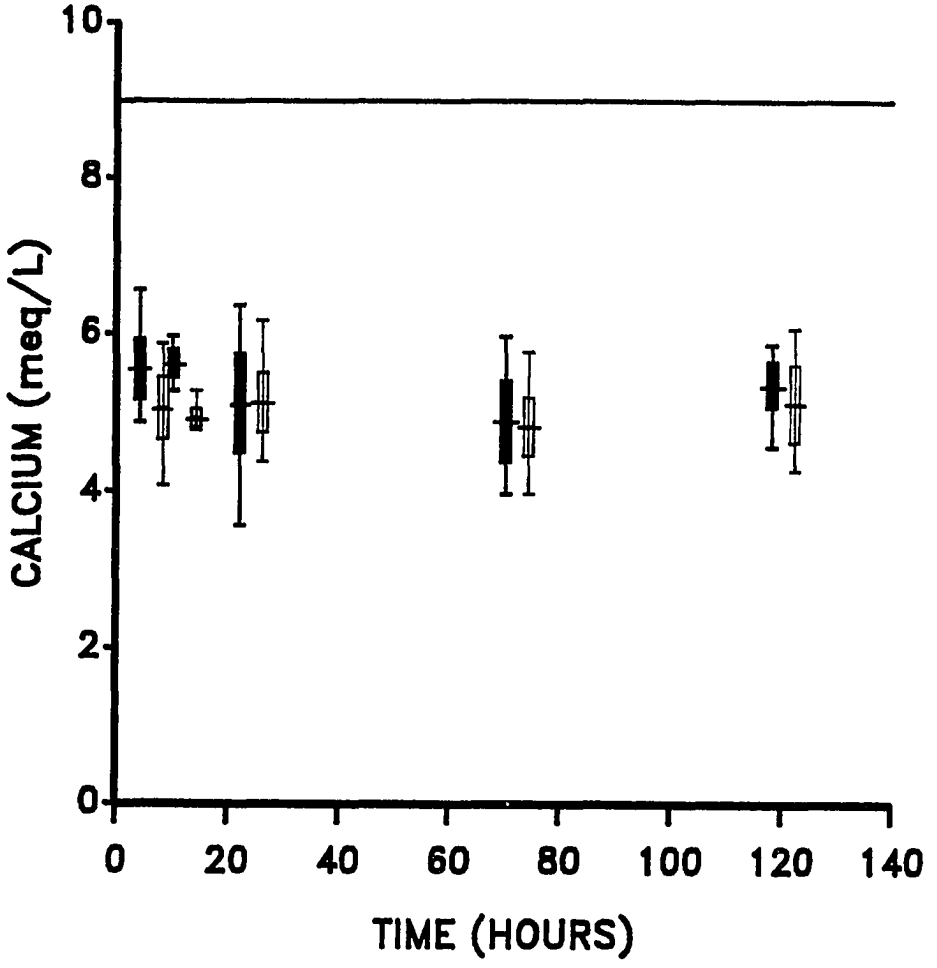

Figure A.12. Plasma calcium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 8 ppt salinity (4 fish from each location at each exposure level). Horizontal line represents upper limit of normal plasma calcium values.

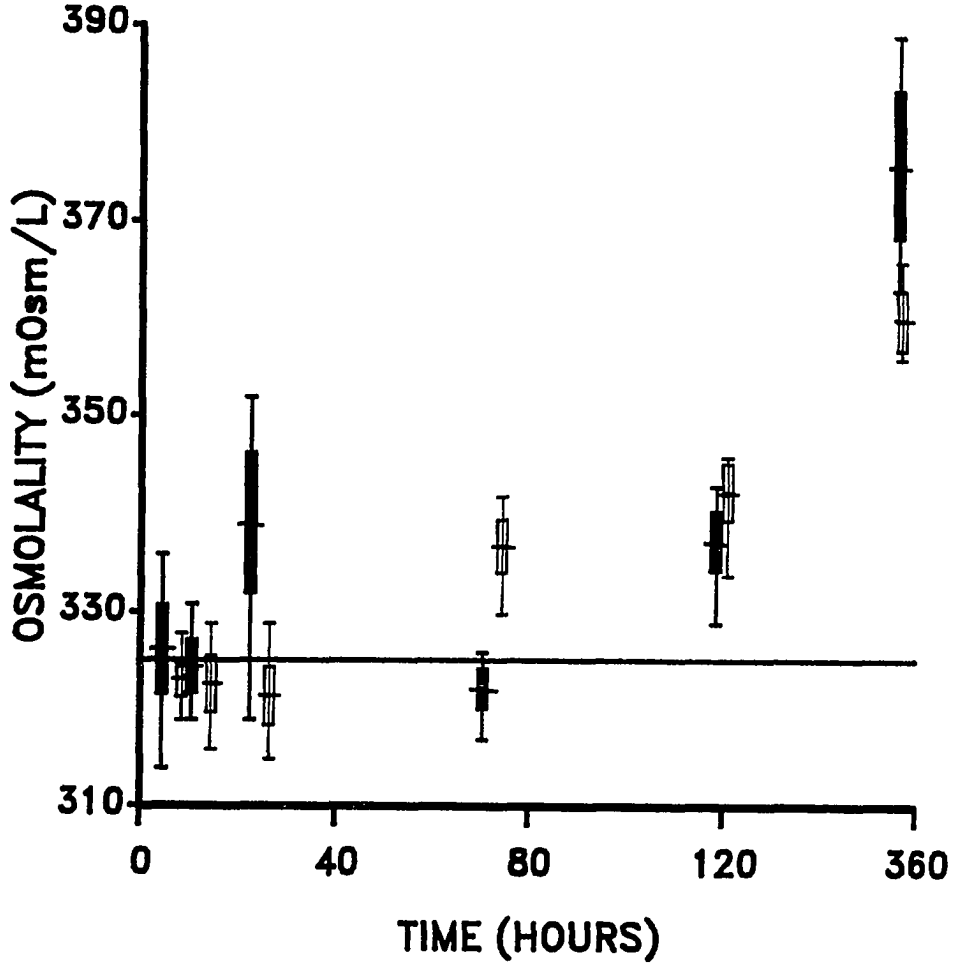

Figure A.13. Plasma osmolality (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, 120, and 336 hours of exposure to 12 ppt salinity (4 fish from each location at each 6, 12, 24, 72, and 120 hours; 3 fish from each location at 336 hours). Horizontal line represents upper limit of normal plasma osmolality values.

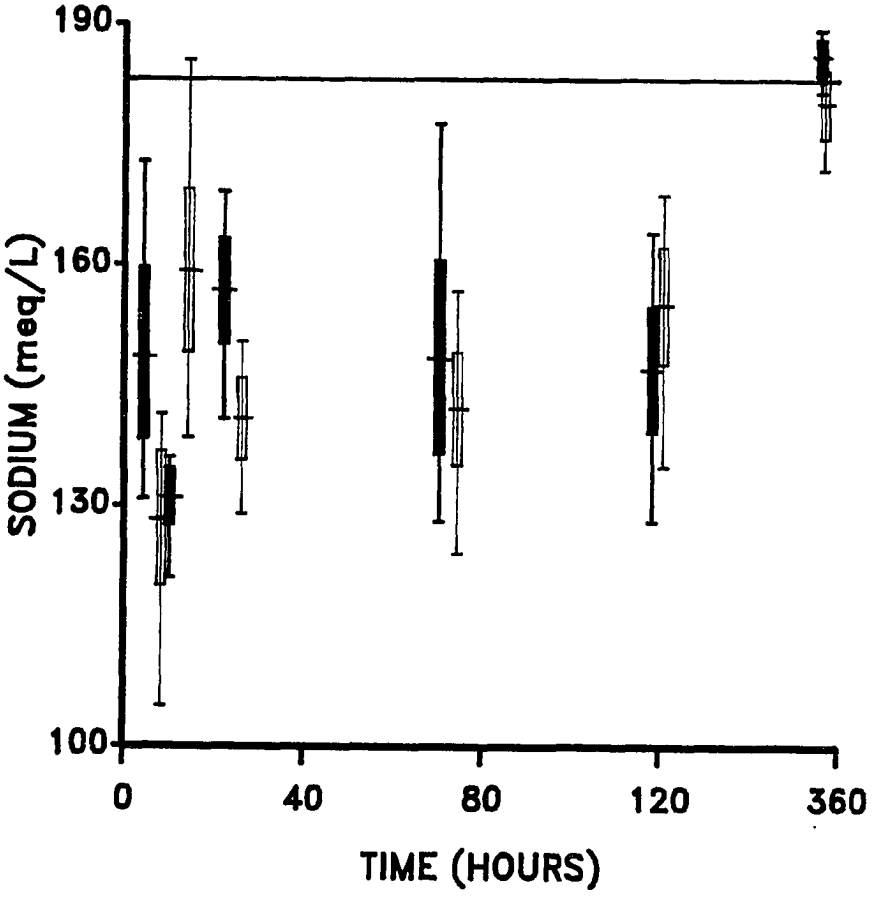

Figure A.14. Plasma sodium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, 120, and 336 hours of exposure to 12 ppt salinity (4 fish from each location at each 6, 12, 24, 72, and 120 hours; 3 fish from each location at 336 hours). Horizontal line represents upper limit of normal plasma sodium values.

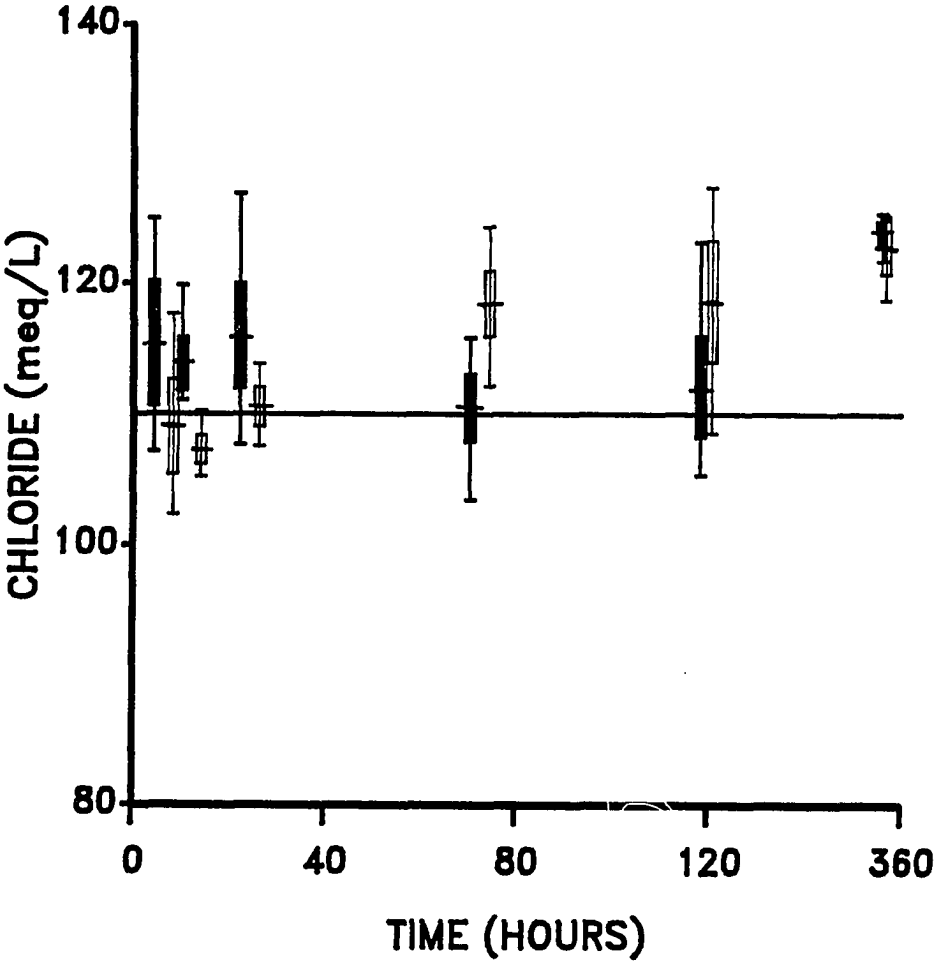

Figure A.15. Plasma chloride (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, 120, and 336 hours of exposure to 12 ppt salinity (4 fish from each location at each 6, 12, 24, 72, and 120 hours; 3 fish from each location at 336 hours). Horizontal line represents upper limit of normal plasma chloride values.

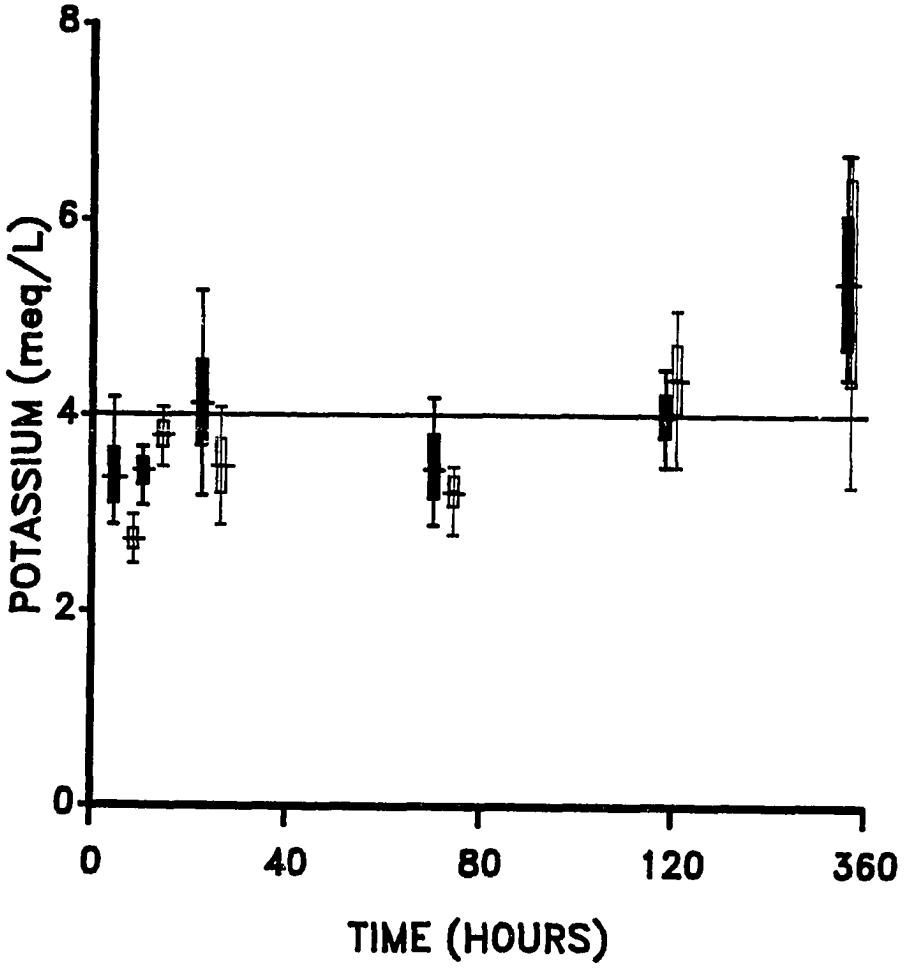

Figure A.16. Plasma potassium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, 120, and 336 hours of exposure to 12 ppt salinity (4 fish from each location at each 6, 12, 24, 72, and 120 hours; 3 fish from each location at 336 hours). Horizontal line represents upper limit of normal plasma potassium values.

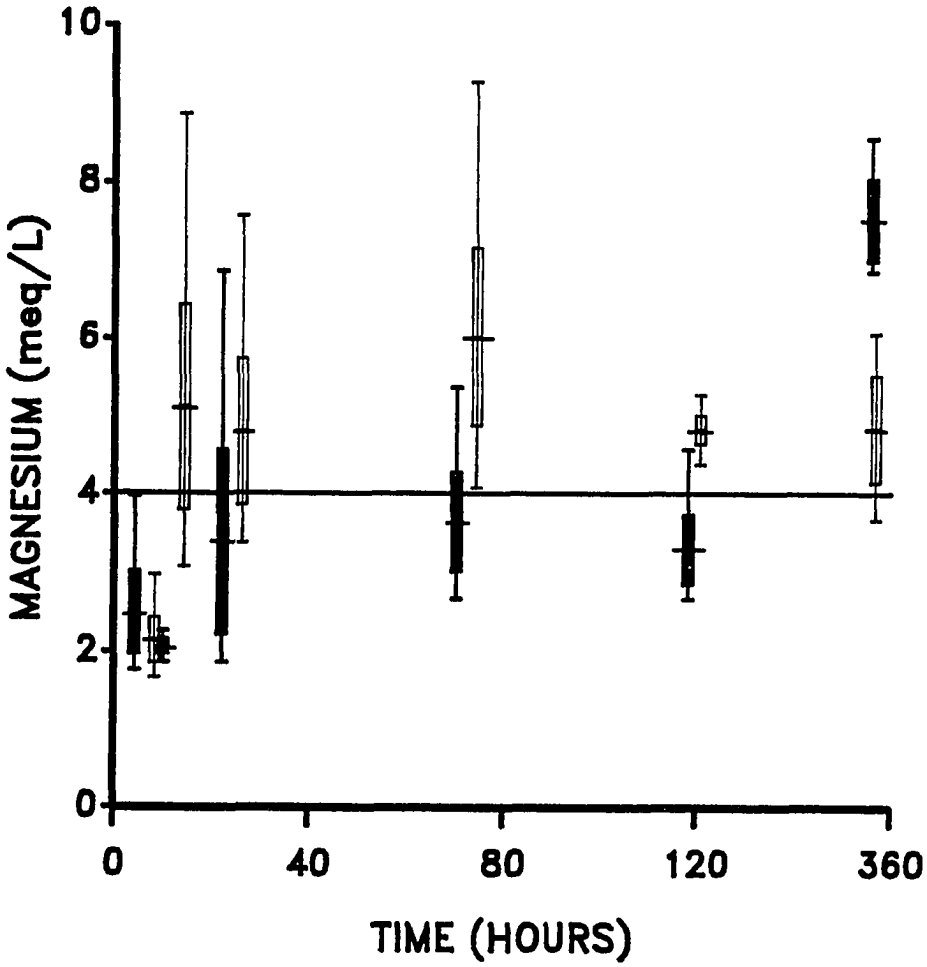

Figure A.17. Plasma magnesium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, 120, and 336 hours of exposure to 12 ppt salinity (4 fish from each location at each 6, 12, 24, 72, and 120 hours; 3 fish from each location at 336 hours). Horizontal line represents upper limit of normal plasma magnesium values.

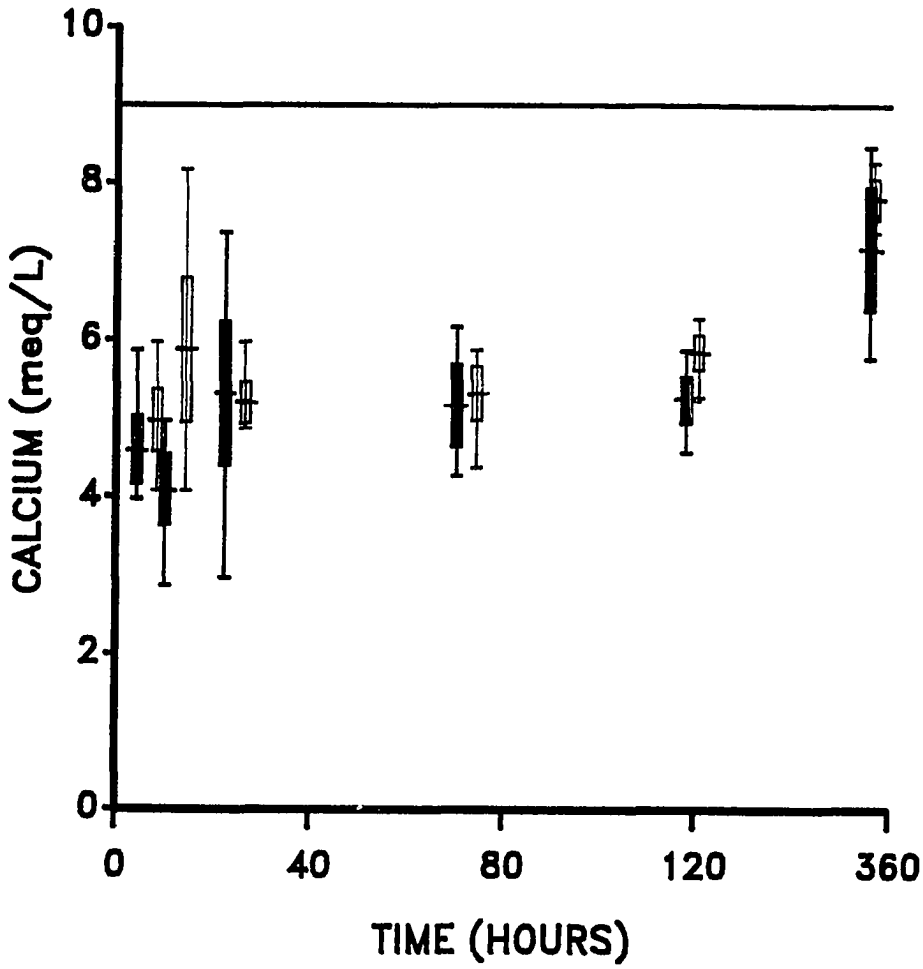

Figure A.18. Plasma calcium (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, 120, and 336 hours of exposure to 12 ppt salinity (4 fish from each location at each 6, 12, 24, 72, and 120 hours; 3 fish from each location at 336 hours). Horizontal line represents upper limit of normal plasma calcium values.

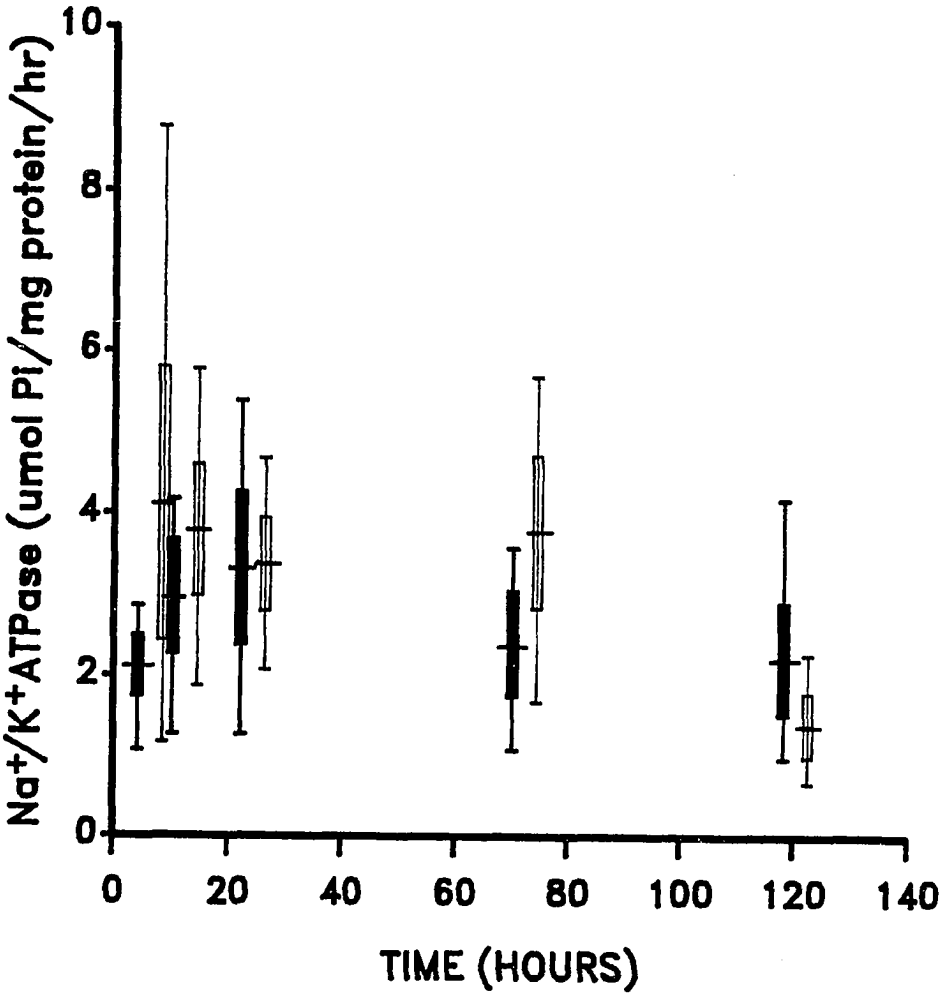

Figure A.19. Gill Na^+/K^+ ATPase activity (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 4 ppt salinity (4 fish from each location at each exposure level).

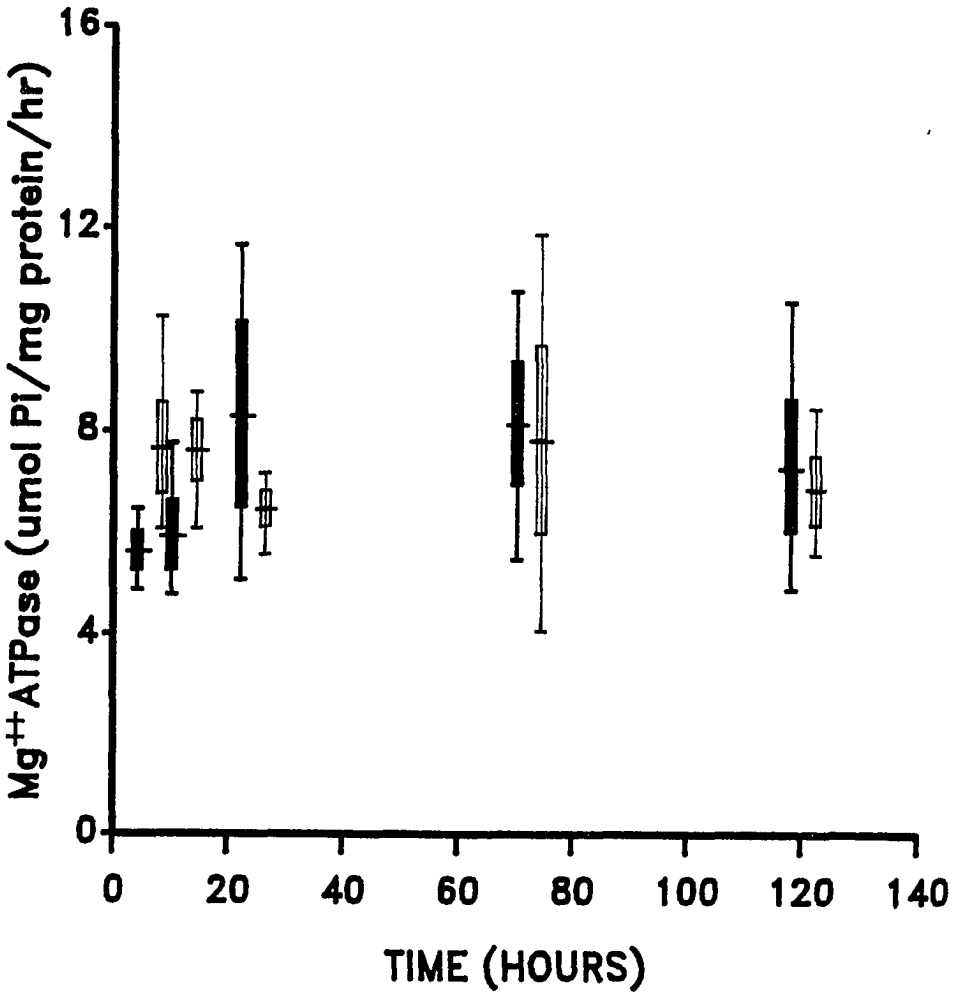

Figure A.20. Gill Mg^{++} ATPase activity (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 4 ppt salinity (4 fish from each location at each exposure level).

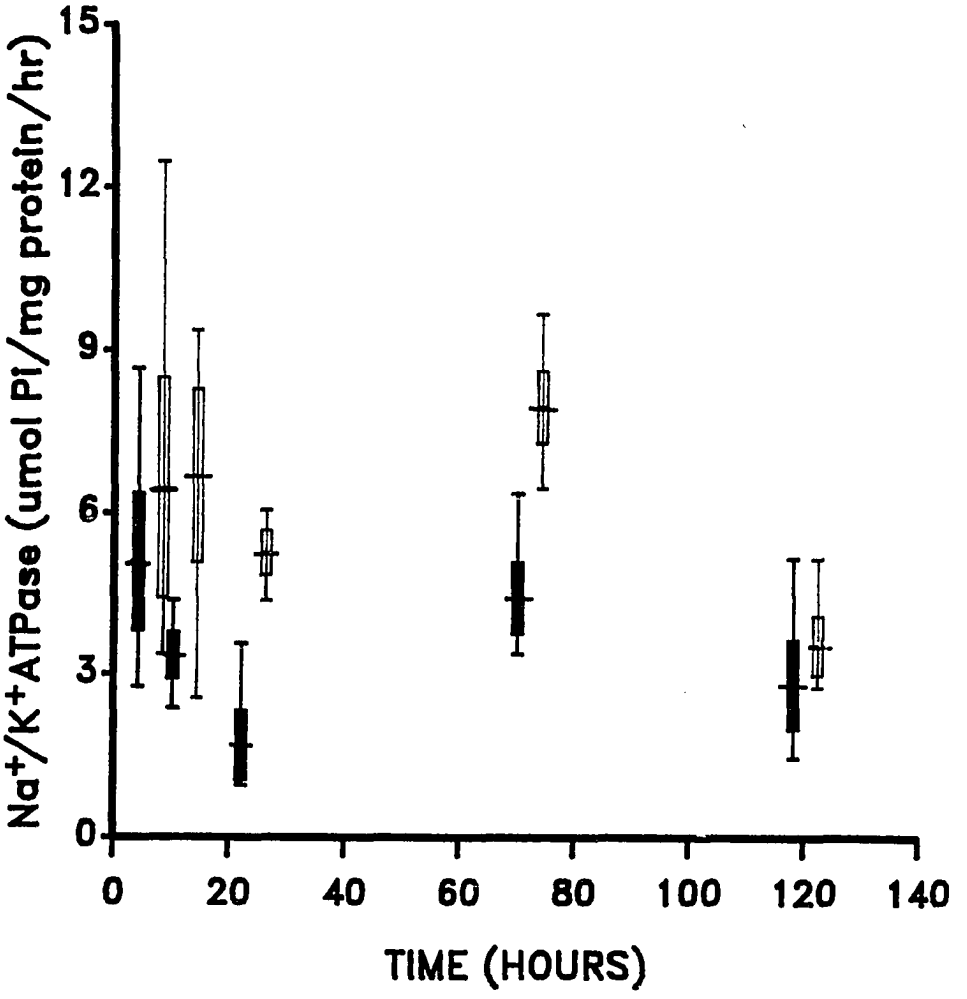

Figure A.21. Gill Na^+/K^+ ATPase activity (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 8 ppt salinity (4 fish from each location at each exposure level).

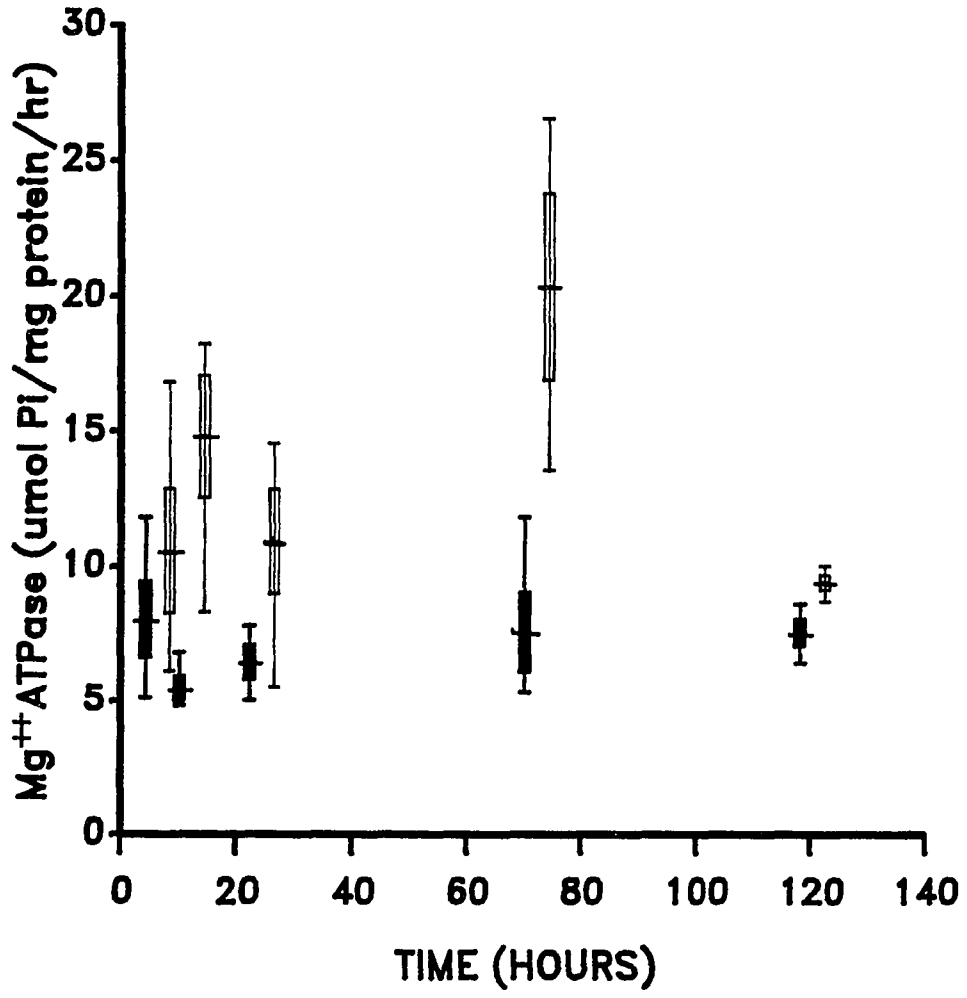

Figure A.22. Gill Mg^{++} ATPase activity (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, and 120 hours of exposure to 8 ppt salinity (4 fish from each location at each exposure level).

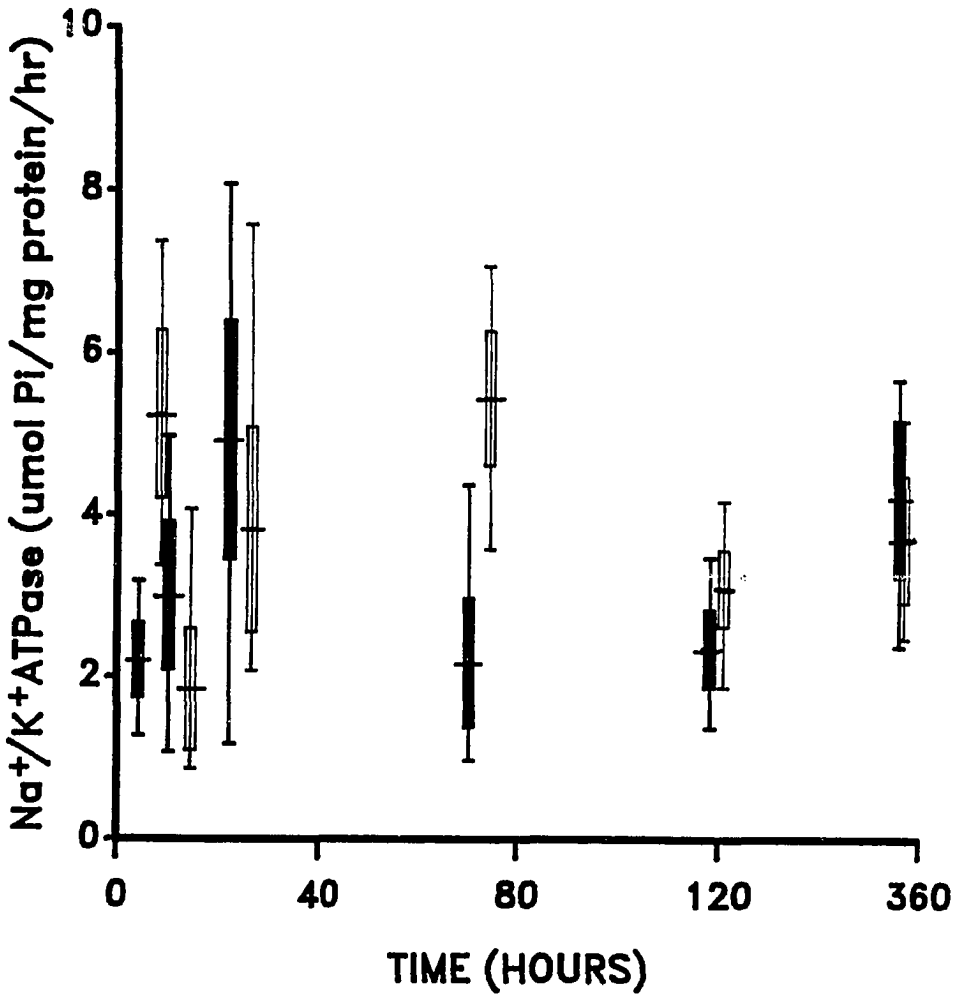

Figure A.23. Gill Na^+/K^+ ATPase activity (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, 120 and 336 hours of exposure to 12 ppt salinity (4 fish from each location at each 6, 12, 24, 72, and 120 hours; 3 fish from each location at 336 hours).

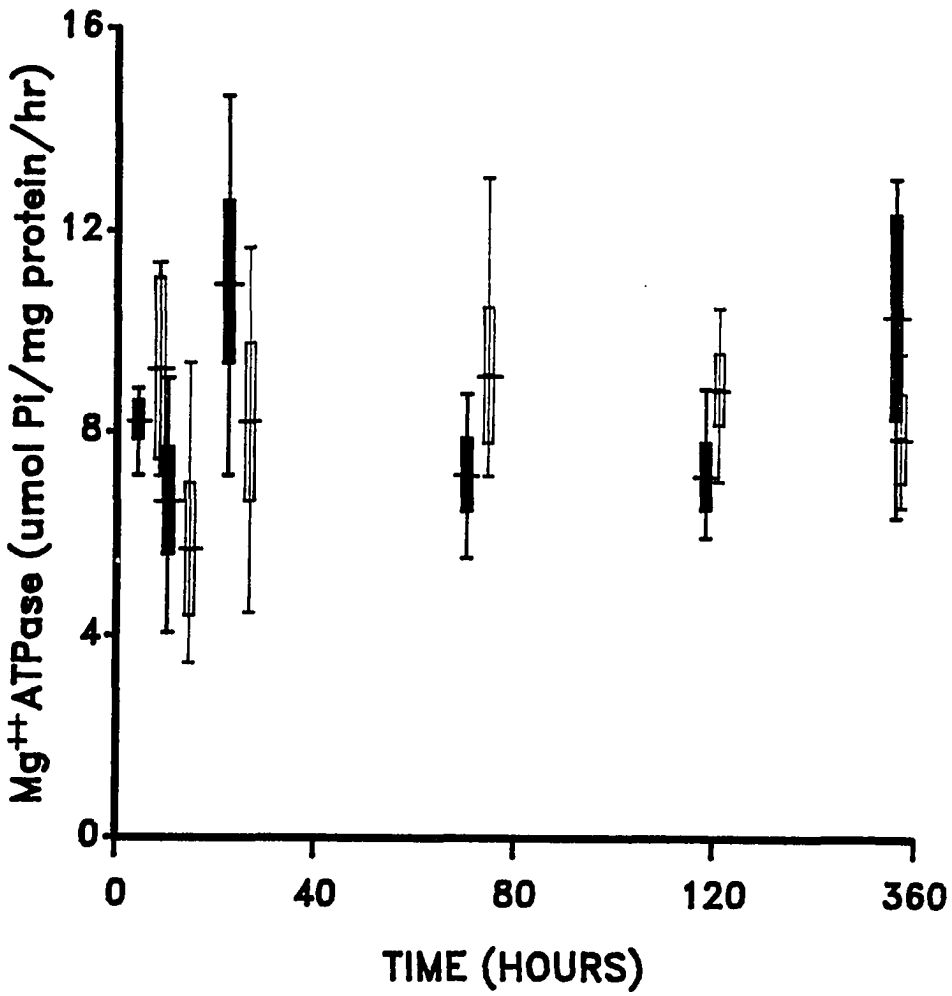

Figure A.24. Gill Mg^{++} ATPase activity (mean ± standard error and range) of largemouth bass from a brackish marsh (solid box) and freshwater lake (open box) at 6, 12, 24, 72, 120 and 336 hours of exposure to 12 ppt salinity (4 fish from each location at each 6, 12, 24, 72, and 120 hours; 3 fish from each location at 336 hours).

VITAE

Michael Rogers Meador was born on August 26, 1958, in Newport News, Virginia. He graduated in June, 1976, from York High School in Yorktown, Virginia.

In September, 1976, he enrolled at Virginia Polytechnic Institute and State University, Blacksburg, Virginia. In June, 1980, he graduated with a Bachelor of Science degree after majoring in Forestry and Wildlife.

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DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Michael R. Meador

Major Field: Wildlife and Fisheries Science

Title of Dissertation: Behavioral and Physiological Adaptations of Largemouth Bass (Micropterus salmoides) to Low-salinity Environments

Approved:

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Date of Examination:

August 30, 1988